ECOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS FOR BREEDING IN THE BELTED KINGFISHER

(*Megaceryle alcyon*)

A THESIS

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INTRODUCTION

The initial objectives of this study were to investigate only the developmental aspects of thermoregulation in the laboratory without regard to the natural history of the Belted Kingfisher. At that time, the problem appeared to be feasible since several thermoregulatory studies had already been conducted with passerine species thereby providing a basis for comparative physiological investigation.

The Belted Kingfisher posed an interesting problem in itself, because (1) it nested in a subterranean burrow, relatively protected from fluctuations in the ambient environment outside the nest, and (2) although kingfishers are not passerines, the young are hatched blind and naked. Such conditions are uncommon among non-passerine birds.

Therefore, it seemed reasonable to hypothesize that due to the uncommon nesting strategy of the Belted Kingfisher, the patterns of growth and the development of temperature regulation may have differed from that of passerine species.

After the first season in the field, what appeared to be occurring in nature did not support the data obtained in the laboratory. These observations strongly implied that in order to gain a better understanding of the adaptations for breeding, it would be imperative to investigate some aspects of the natural history of kingfishers.

In final analysis, I can only state that had this study been confined to its initial objectives, a great deal of information would have been lost. Moreover, I feel that more questions have been raised than have been answered, and that the adaptations for breeding in the Belted Kingfisher remain open for further investigation.

METHODS AND THE STUDY AREA

The field observations and laboratory experiments reported in this study were conducted in Itasca State Park, Minnesota and the surrounding region during the springs and summers of 1970, 1972, 1973, and 1974. Lakes, ponds and streams are plentiful throughout the uneven terrain formed by Pleistocene glaciation. Vegetation in the study area is diverse since the Itasca Region lies at the confluence of three major North American biomes. In addition, the vegetation within the park has been relatively protected since the late 1890's, whereas adjacent lands have been subjected to agricultural and lumbering operations.

Natural history observations were made with 7X binoculars and a 30X spotting scope throughout the daytime and evening hours from 3 May through 15 August. Occasional observations were made during the winter and early spring.

Age of nestlings was recorded as days after hatching. Eggs and nestlings were weighed with a dietetic scale, and culmen length and wing length were measured with standard calipers. Additional equipment used to facilitate natural history observations are discussed within the text.

Procedures for the investigation of temperature regulation are reported in Part II of this study.

KINGFISHERS AND THEIR ALLIES

Among the 27 orders of birds of the world, the Coraciiformes represent a taxonomic group comprised of 10 defined families (Wetmore, 1960). Distributed throughout the tropical and temperate regions of the earth, but absent in the polar regions, the order exhibits its greatest development in the Old World. Only one family within the Coraciiformes, the Alcedinidae, is represented in both the Eastern and Western Hemispheres.

The Alcedinidae or family of kingfishers includes 87 species, only six of which occur in the New World. The greatest species richness within the family occurs in the Australian and Oriental zoogeographical regions of the Old World.

Two subfamilies constitute the Alcedinidae, the Daceloninae and the Alcedininae (Ridgway, 1914). The Daceloninae or forest kingfishers are not entirely water birds, but several species inhabit forests and savannahs. Forest kingfishers are confined to the Eastern Hemisphere. Their diet consists of insects, fish, amphibians, reptiles, young birds, and small mammals. As is typical of all the Coraciiformes, the forest kingfishers nest in holes, sometimes excavated in soil but at times in hollow trees or in termite nests (Austin, 1961).

The Alcedininae or fishing kingfishers differ from the forest kingfishers primarily by shape and structure of the bill. All are birds of watercourses, ponds, and lakes. Their nesting habits typically include a subterranean burrow excavated by the birds. Although fishing kingfishers have occasionally been known to feed on amphibians, reptiles, birds, and small mammals, the primary diet consists of fish and aquatic arthropods.

THE BELTED KINGFISHER

The Belted Kingfisher (Megaceryle alcyon) is the only member of the Alcedinidae that breeds in the temperate zones of North America. The breeding range extends from Alaska to Labrador and south to include most of the middle and southern regions of the United States.

Two subspecies are recognized, the Eastern Belted Kingfisher, Megaceryle alcyon alcyon (L.), and the Western Belted Kingfisher, Megaceryle alcyon caurina (Grinnell) (A. O. U., 1957). Although the subspecies are quite similar, Grinnell (1910) believed that the overall larger body size, longer length of the remiges and longer culmen length in M. a. caurina warranted taxonomic sub-classification. Measurements of culmen length of adult specimens that I obtained from the research collection of the National Museum of Natural History, Washington, D. C., indicate that a significant difference in culmen length does exist between the two subspecies ($p < .01$; n=41).

Sexual dimorphism in the Belted Kingfisher readily permits field identification. Whereas males only have a single blue band extending across the breast, females have an additional chestnut band extending across the breast and continuing along the flanks. All other external characteristics of the two sexes are essentially indistinguishable. Culmen length measurements of both living birds and preserved specimens indicate no significant difference between the sexes ($p < .01$; n=32).

In this study, the body weights of 14 adult birds ranged from 140 grams to 169 grams with an average weight of 147.1 grams. Within pairs, body weights were occasionally equal, males were heavier than females or vice versa.

In northern latitudes kingfishers are for the most part migratory since their subsistence depends primarily on fish which must be obtained from open waters. In the Lake Itasca Region, ice forms on the lakes by early December and does not melt until mid-April. However, in shallow running waters where swift currents prevail, the water may remain open throughout the winter.

During the winter of 1973-74, a male kingfisher was observed from 31 December through late March at the headwaters of the Mississippi River. Although temperatures were as low as -45° F. (-43° C.), the bird did not appear to suffer any detrimental effects due to ambient temperature. The river remained open for approximately one-quarter mile downstream from the outlet of Lake Itasca, and shiners (Notropis sp.) were abundant in the open water.

Regurgitated pellets were found beneath several fishing perches along the banks of the river. A dense stand of balsam fir stood beside the river where the bird apparently roosted. Snow beneath the trees was riddled with excreta and pellets. Examination of several pellets revealed only fish bones and scales.

No further observations of the bird were made during April, and by early May, no birds were observed in the area.

ARRIVAL AND COURTSHIP ACTIVITIES

In the Itasca Region, early migrant kingfishers are first observed in mid-April when the lakes and ponds are beginning to thaw. Adults continue to arrive through early May (Figure 1). White (1953) reported that the main migration in the maritime provinces of Canada was during the last 10 days in April.

My observations from central and northern Minnesota indicate that males return before females. During the first week of May, several lakes in the Itasca Region that traditionally supported kingfishers were only occupied by males. However, by the second week in May, females had arrived and courtship commenced almost immediately.

Little is known of the courtship behavior of the Belted Kingfisher. In the Itasca Region, observations of complete courtship sequences were often hindered by tall trees and irregular terrain.

No elaborate pre-copulatory displays were ever documented. On seven occasions when copulation was observed, the male always flew to the female's perch, paused briefly and proceeded to mount her. During copulation, the male maintained balance by fluttering his wings while treading on the female's back. The female assumed a crouched posture and retracted her head. Cloacal contact occurred after the female cocked her tail to the side. Copulations lasted from 7 - 12 seconds.

After copulation, the male, followed by the female, left the perch and encircled the lake. As the pair circled over the lake, the male occasionally soared and dipped close to the water as the female followed. The female then returned to a perch along the shore, but the male continued in an upward ascending flight.

After reaching an altitude of 200 - 300 feet over the water, the male paused briefly and proceeded to execute a dive, often somersaulting in the descent. The somersaults appeared to be head-first and at times were preceded by stalling in mid-air. Just before reaching the water, the male pulled out of the dive and into an ascending glide in which the wings were fully extended and the patches of white on the remiges were immediately obvious. Sometimes, the female joined the male and the pair continued to circle the lake in the same manner as described above.

Although the Belted Kingfisher is reputedly known for its characteristic rattle, after copulation a "mew" call quite different than the typical rattle was given as the pair circled the lake. The "mews" were given at regular intervals, although it could not be determined whether both sexes were vocalizing. An additional shrill decrescendo rattle was occasionally given during the chases, but the call was not limited to post-copulatory displays. The same vocalization was given during nest excavation and during interactions with other kingfishers.

On several occasions, during the early morning hours, three birds (two males and one female) were observed circling and chasing one another several hundred feet over a lake and/or nesting area. Somersaults and diving were common, and the characteristic rattle as well as the decrescendo rattle were given by members of the trio. White (1953) reported similar behavior in groups of three or more birds but offered no explanations for it.

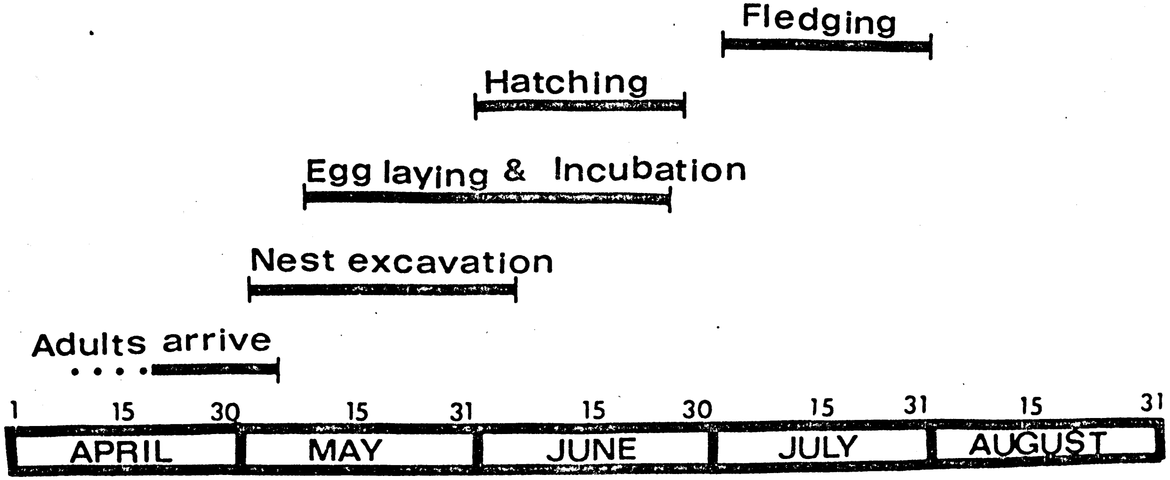
The sequence terminated when the three birds left an area and eventually only a pair returned. These observations led me to the same conclusion as Salyer and Lagler (1946) who found that such chases were due to intrusions by bachelor birds infringing on the territory of a mated pair.

The frequency of courtship activity appeared to decrease after the initiation of nest excavation. However, such observations require further qualification since the nesting area was not always adjacent to the fishing area.

Figure 1

Breeding phenology of the Belted Kingfisher in the Lake Itasca Region, Minnesota.

BREEDING PHENOLOGY OF THE BELTED KINGFISHER IN THE LAKE ITASCA REGION – MINNESOTA



NEST SITE SELECTION

The Belted Kingfisher has traditionally been recognized as a bird of ponds, rivers and streams where nesting holes are excavated in natural banks formed by water erosion. However, in the Lake Itasca Region natural nesting sites are limited by the low shorelines of lakes and the densely vegetated banks (Cornwell, 1963). A similar habitat was noted by Rowan (1921) at the Lake of the Woods, Manitoba, where kingfishers neither nested along the lake shores nor on the scores of islands that were comprised largely of rock. Furthermore, White (1953) maintained that in the maritime provinces, the availability of nesting sites limited the abundance of kingfishers, and von Haartman (1971) discussed the effects of available nesting sites on hole-nesting species.

Kingfishers prefer a nearly vertical bank of exposed soil and devoid of vegetation for nesting. Consequently, the breeding population in the Itasca Region would appear to be limited not by the plentiful waters that should assure the species of ample food resources, but rather by suitable nesting sites. The current population of breeding kingfishers appears to be dependent on artificial nesting habitats created by human incursion (Hamas, 1974).

During the breeding seasons of 1970, 1972, 1973, and 1974, 29 nests (88%) were excavated in habitats created by human disturbance (Figure 2). Most of the nests were in gravel pits, sanitary land fills, and along road cuts. Only four nests (12%) were found in natural embankments. Nest sites were as far away as 1.5 miles from a pair's feeding territory, and regardless of the availability of suitable banks for nest excavation, only one pair of birds occupied a given nesting habitat.

Results from banding indicate that at least female kingfishers return to the same nesting habitat used in previous years. An adult female that was banded in June, 1973, returned to the same nest site in 1974 but did not nest in the same burrow as in the previous year. The status of her mate was never determined, however, since the nest was deserted and a colored leg band was never observed on the male. Evidence also exists that first year birds return to the natal locality during their second spring (White, 1953), although such observations were never documented during this study.

Although kingfishers nest solitarily, they occasionally select nest sites in colonies of Bank Swallows or Rough-winged Swallows. Sometimes, Rough-winged Swallows attempt to build a nest in an incomplete kingfisher burrow, but the persistent daily digging by the kingfisher is sufficient to discourage the swallows from re-nesting. Kingfisher burrows from previous years are often used by Bank Swallows and/or Rough-winged Swallows. For undetermined reasons, a pair of kingfishers occasionally abandons a partially excavated burrow and swallows occupy it at once. Lunk (1962) similarly noted that in southeastern Michigan Rough-winged Swallows took advantage of unoccupied kingfisher burrows for nesting.

Tenacity of the nest site is strong once nest excavation has begun. In 1974, a pair of birds nested in a gravel pit that had several available nest sites. In order to determine the persistence for nesting in a particular habitat, the nest was destroyed when it was near completion. Two days later, the birds started to dig another nest on the opposite side of the gravel pit. Again, the nest was destroyed after a couple days of digging, but the birds attempted a new nest on the following day. Four attempts at nesting were discouraged and the birds were finally permitted to complete the fifth nest. Although the nest was completed, eggs were laid, and incubation was initiated, the nest failed when a bulldozer went through the bank and killed the incubating female. The male was never observed again, and the gravel pit was not occupied by kingfishers for the remainder of the breeding season.

Figure 2

Nest sites of the Belted Kingfisher in the Lake Itasca Region.

Nest Sites of the Belted Kingfisher in the Lake Itasca Region

year	gravel pits & sanitary land fills	road cuts	natural sites	total
1970	3	2	2	7
1972	6	1	1	8
1973	4	5	1	10
1974	4	4	0	8
total	17	12	4	33
%	52	36	12	100

THE NEST

The Belted Kingfisher typically nests in a subterranean burrow that is excavated entirely by the adult birds. Since the availability of nest sites is often at a premium, the species has rarely been known to nest in the open tops of decayed stumps (Beyer, et. al., 1908) and in decayed stubs of trees (Forbush, 1927; Sutton, 1928).

Both male and female participate in excavation of the nest. Most of the digging, particularly during the early stages of excavation, is by the male, while the female continuously calls from a nearby perch. Mousley (1938) observed that the male spent twice the time digging as did the female. Timed observations of nest excavation by three pairs of birds in Itasca Park showed that the time spent at nest excavation by males was 1.7 times longer than spent by females.

The initial stages of nest excavation commenced during courtship when a pair flew to a suitable nest site, and the male landed on a bank where vertical slashes in the soil were made with the bill. The female remained in a nearby tree giving the characteristic rattle and an occasional decrescendo rattle. Perhaps the decrescendo rattle functioned as a mechanism by which the pair bond was reinforced. For several minutes, the male flew back and forth from the nest site to the general vicinity of the female. Occasionally, the female flew to the fresh diggings while the male remained on a nearby perch and rattled.

On the first day of excavation, a tunnel may extend 11 inches into a bank. Digging was usually confined to the early morning hours, but a pair sometimes returned to dig during the early evening. The time required for completion of the nest was from 4-7 days, and appeared to be dependent on the consistency of the soil. No nest excavation was observed during periods of heavy rain.

The completed nest burrow extended from approximately 3-5 feet into a bank. The tunnel entrance was never more than 20 inches from the top of a bank, although some banks were as high as 30 feet (Figure 3). Mousley (1938), White (1953), and Cornwell (1963) similarly noted that the nest entrance was rarely more than two feet from the top of a bank.

The distance from the top of a bank to a nest entrance may be a strategy by which potential predators are avoided. Possibly the tunnel is sufficiently distant from the top of a bank that the probability of its discovery is reduced. However, should a nest be discovered by a mink or weasel, the dimensions of the tunnel would permit easy entry (Figure 3). Predators from the bottom of an embankment may likewise have difficulty ascending a vertical bank or in the process of doing so, may expose themselves to their own predators.

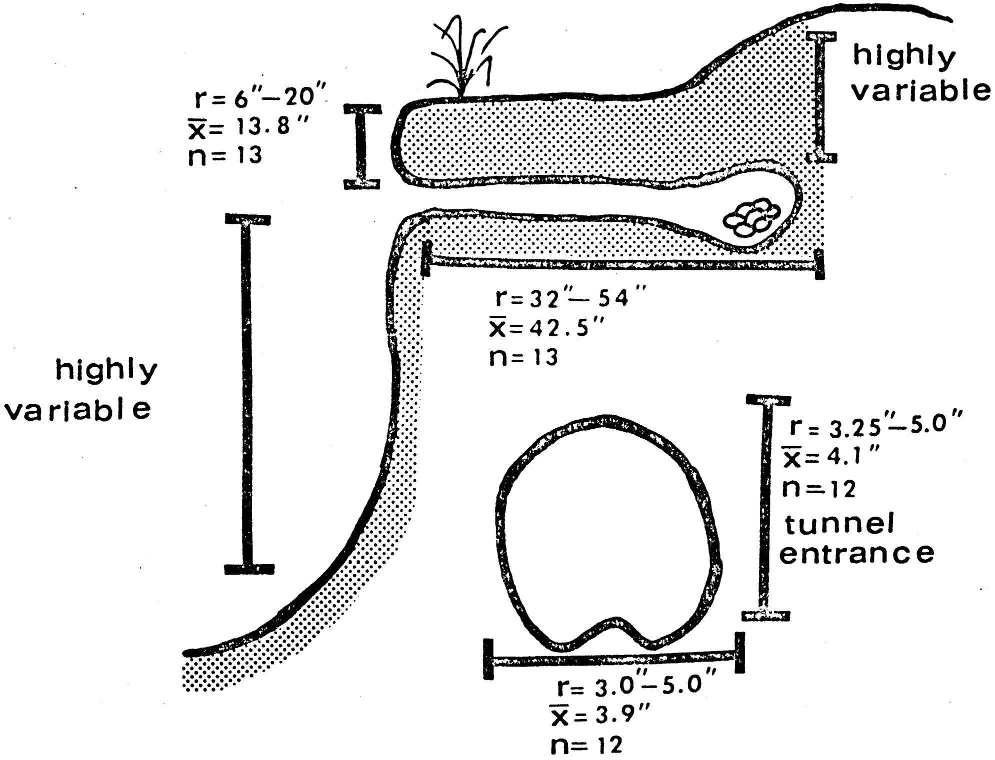
The actual nest of the kingfisher consists of a roughly spherical chamber from 9-10 inches in diameter. No nest lining is utilized and reports of twigs and grasses in the nest chamber (Rowan, 1921; Gabrielson and Lincoln, 1959) are probably due to the nest building attempts of swallows during periods when adult kingfishers are not at the nest. At several nest sites, a pair of Rough-winged Swallows circled the nest as the kingfishers were digging.

In the nesting area, activity of the pair is greatly reduced after completion of the nest. Occasionally the pair returns to the nest site, but the constant vocalizing associated with nest excavation ceases. If one bird enters the nest, there is no calling from the bird that remains outside the nest.

The time between completion of the nest and deposition of the first egg may be one week. During this time, the female may be building up reserves for egg laying, or the apparent "desertion" of the nest may be a mechanism by which predation is avoided. The constant vocalizing associated with nest excavation may attract undetected predators. Therefore, if eggs were laid immediately after the nest was complete, the energy invested in breeding could be lost.

Figure 3

Nest dimensions of the Belted Kingfisher.


r = 6"–20"
x̄ = 13.8"
n = 13
highly variable
highly variable
r = 32"–54"
x̄ = 42.5"
n = 13
r = 3.25"–5.0"
x̄ = 4.1"
n = 12
tunnel entrance
r = 3.0"–5.0"
x̄ = 3.9"
n = 12

EGG SIZE AND CLUTCH SIZE

Eggs of the Belted Kingfisher, like most directly adapted hole-nesting species, are white (von Haartman, 1957). In shape and texture, they are ovate and glossy. Bent (1940) found that the standard measurements of 54 eggs averaged 33.9 mm (length) by 26.7 mm (breadth). Extreme measurements were 30.8 and 36.8 mm (length) by 25.4 and 27.9 mm (breadth). The average measurements that I made on 10 sets of eggs ($n = 70$) from the research collection of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, were 33.5 mm (length) by 26.8 mm (breadth). The range of measurements was from 30.4 - 36.1 mm (length) by 25.2 - 28.1 mm (breadth).

Measurements from three sets of eggs ($n = 21$) from the Itasca Region averaged 35.3 mm (length) by 27.8 mm (breadth) with extreme measurements being 32.5 mm and 36.8 mm (length) and 27.1 mm and 29.0 mm (breadth). The mean weight of fresh eggs ($n = 24$) from the Itasca Region was 11.3 grams (range 10-14 gms.).

Clutch size of the Belted Kingfisher usually consists of 5-7 eggs, with a clutch of seven being the most common. In the Itasca Region, 70% of the nests ($n = 17$) contained seven eggs (Figure 4). Kingfishers rear one brood per year in northern temperate regions, but in the southern United States, kingfishers have been known to be incubating eggs in March and possibly raise two broods in one year (Sharpe, 1868). However, two broods appear to be extremely uncommon, if any basis for such observations exists at all. Skutch (1957) found no indication of a second brood in the neotropical Amazon, Green, and Ringed Kingfishers, although Moreau (1944) reported that the African Half-collared Kingfisher does rear two broods a year.

The adaptive significance of clutch size in birds has been the subject of several hypotheses, all of which are singly inadequate to explain existing data. The problem with many of these hypotheses lies in the fact that generalizations can be dangerous when ecological factors associated with the breeding strategies of individual species are overlooked. Cody (1966) has discussed the factors that determine clutch size in relation to the environment.

The Belted Kingfisher lays seven eggs, the significance of which remains open to speculation. There is little acceptance of the hypothesis that a bird may be physiologically limited from laying more eggs, yet several examples exist that support or oppose the theory. During the course of this study, only one attempt to re-nest was observed after destruction of a nest containing seven eggs. The second clutch contained six eggs. Skutch (1957) also found that an Amazon Kingfisher re-nested after destruction of a nest containing four eggs; the second clutch contained three eggs. Although many Belted Kingfisher nests were deserted due to human interference, there were no further attempts to nest again.

The fact that one pair did re-nest suggests that clutch size in kingfishers may not be physiologically limited, at least during the first attempt at laying. However, it would be advisable to plan experiments by which eggs of a clutch would be removed in order to determine whether the female would continue laying.

That clutch size is limited by the number of eggs an adult can cover is another hypothesis that appears to be inadequate for many birds (Cody, 1966). Observations of incubating kingfishers indicated that it would be difficult to cover more than seven eggs adequately. The spatial arrangement of eggs was such that during incubation the outer surfaces were occasionally exposed and the wings were lowered over the exposed shells. The feathers probably helped to conserve heat.

It is rather doubtful that clutch size of kingfishers is a response to balance mortality. As Lack (1947, 1949, 1954) pointed out, no such mechanism has been shown. If such were the case, however, the basic postulate of natural selection would be subject to major revision.

One of the widely accepted theories regarding the significance of clutch size in birds emerged from the work of Lack (1947). The theory contended that clutch size was determined by the average maximum number of young for which the adults could procure sufficient food. Lack's hypothesis has gained wide support through data obtained from many avian species, and it is indeed difficult to dismiss the relationship of food supply to breeding strategies. However, Skutch (1949) reported that tropical birds do not rear as many young as they could nourish.

Likewise, the Belted Kingfisher does not appear to rear as many young as it could nourish. Observations of feeding rates suggest that the adult birds could supply more food than they actually do (Figure 12). Therefore, it seems unlikely that clutch size of the Belted Kingfisher is limited by food, particularly in the Itasca Region.

Clutch size of the New World kingfishers increases with latitude (Belcher and Smooker, 1936; Bent, 1940; Skutch, 1957; Lack, 1968). Lack (1947) interpreted such a trend on the basis of food limitation and day length. In areas where longer day length prevails during the breeding season, the adults are afforded more time for finding food and subsequently raise larger broods. Cody (1966) surmised that energy in the temperate zones is invested to increase reproductive rate whereas in the tropics, the carrying capacity of the habitat dictates smaller clutch size.

No single theory regarding clutch size is singly applicable to the Belted Kingfisher. The significance of clutch size then is probably a compromise of the foregoing theories. The fact that the typical clutch consists of seven eggs and not some other number remains unexplained. That clutch size is limited by the number of eggs that can be covered by an adult seems to be a plausible factor limiting the number of eggs laid, and whether kingfishers are physiologically limited from laying more eggs is not well documented.

Figure 4

Clutch size of the Belted Kingfisher in the Lake Itasca Region.

clutch size	1970	1972	1973	1974	total
5 ○○○○○	—	1	—	1	2
6 ○○○○○○	—	1	1	1	3
7 ○○○○○○○	2	1	5	4	12

INCUBATION

Considerable controversy exists in the literature regarding the length of incubation in the Belted Kingfisher as well as the role of the male and female in incubating the eggs. Roberts (1932) described incubation as lasting from 16-17 days. However, Bent (1940), Gabrielson and Lincoln (1959), and Wetmore (1964) maintained that the incubation period was 23-24 days. Skutch (1945) reported that the incubation period for three Belted Kingfisher nests was 22 days, and in the Lake Itasca Region, the incubation period for three nests was observed to last 22 days.

Kingfisher eggs usually hatch synchronously within a 12-18 hour period. In one nest, however, hatching was asynchronous. In this nest containing seven eggs, three hatched after 22 days of incubation, but a fourth egg hatched two days later. The remaining eggs never hatched and were infertile. All nestlings survived and fledged at the same time.

When the last egg of a clutch is laid, incubation begins immediately. Most of incubation is performed by the female, although the male does take an active role. Only the female, however, possesses a brood patch.

Since incubation by kingfishers is difficult to observe, a 24 hour recording device was coupled with a nest by means of a trip mechanism placed at the entrance of the nest burrow. Therefore, when an adult left or entered the nest, the timing apparatus recorded a deflection on recording paper. In addition, the nest was periodically examined throughout the day in order to determine which adult was incubating.

Monitoring the nest by these methods demonstrated that the female remained in the nest burrow throughout the night and during most of the day. Early in the morning, the male relieved the female while she probably went to the fishing territory in order to feed. The female returned to the nest within an hour and remained there for the remainder of the day. In the evening, the male returned to the nest but remained only briefly, usually about five minutes. The male may have been feeding the incubating female during this interval.

Other recordings of incubation that failed to record for an entire 24 hour period indicated that the male sometimes spent 2-3 hours on the eggs after relieving the female. Nevertheless, most of incubation was performed by the female.

NESTING SUCCESS

Margaret Nice (1937) found that in a number of hole-nesting species, 65% of the eggs resulted in fledglings whereas among open nesting species, only 43% were successful. Likewise, Lack (1968) and von Haartman (1957) have discussed further the advantages and adaptations related to hole-nesting strategies.

One advantage of being adapted for hole-nesting is the reduced frequency of predation. During the course of this study, no kingfisher nests failed due to predation, although potential predators occurred in the general vicinity of the nests. Garter snakes (Thamnophis sp.) were the only notable reptilian predators that could have destroyed eggs, but any predator seeking access to the eggs would have had to deal with the attacks of an incubating adult. In a nest that had been opened from behind the nest chamber, a Microtus gained entry to the nest and was speared several times by the incubating adult.

Known mammalian predators of kingfisher nests include skunks and weasels (Bent, 1940; White, 1953). Skunks and badgers were observed near nests but never attempted to disturb them. Even after hatching, when the nestlings would appear to be extremely vulnerable due to their vocalizing, nests were not disturbed by predators. Perhaps the exposed entrance of the nest on a bare soil surface deters potential predators, although weasels are known to be regular predators on Bank and Rough-winged Swallow nests (Lunk, 1962).

If the colonial nesting habits of swallows tend to attract predators, the solitary nesting habits of kingfishers may be a mechanism by which predation is avoided. This hypothesis is consistent with my observations of one kingfisher nest in a suitable nesting habitat regardless of the size of the habitat and the availability of food resources.

Kingfishers will readily desert the nest, particularly during egg laying and the early stages of incubation. Several nests were deserted due to human interference and extreme caution had to be observed before eggs hatched. After hatching, however, young birds could be removed from the nest for extended periods of time without jeopardizing the success of the nest. As long as one nestling remained in the nest chamber, the adults continued to respond to its begging calls by bringing fish to the nest.

Since kingfishers represent a terminal consumer in aquatic food webs, it would be reasonable to suspect that hatching success might be affected by chlorinated hydrocarbon residues. Fox (1974) has shown that egg shell thickness of eggs collected in 1951 and 1962 was just significantly thinner ($p < .05$) than eggs collected prior to the widespread use of insecticides. Egg shell thickness was not measured in the present study, but hatching success of those nests not deserted due to human intervention was 86.95% ($n = 92$ eggs). Those eggs that did not hatch were rotten and showed no evidence of embryo development. In no instance did an entire nest fail.

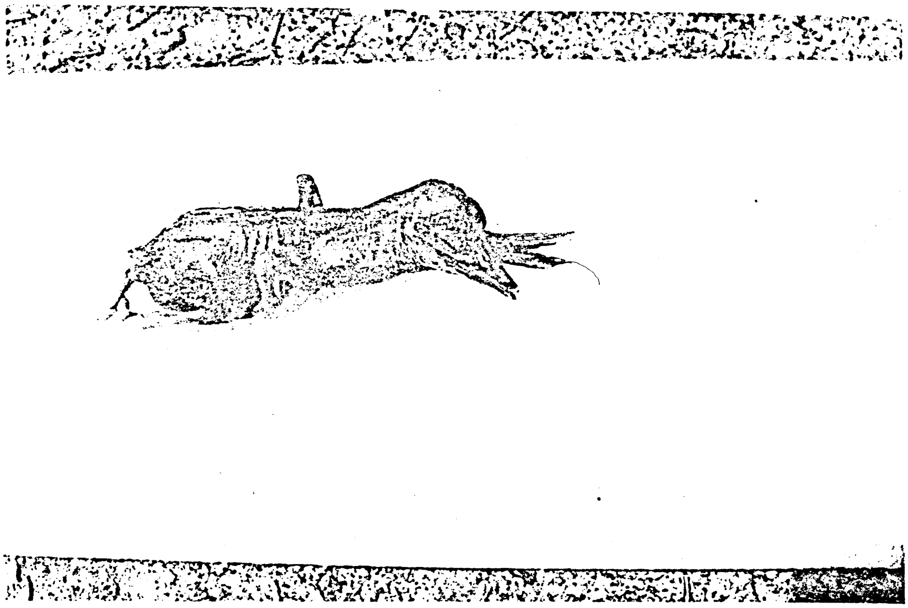
Mortality of nestlings occurred early in the nestling period. The greatest cause of nestling mortality, as with nest failure, was human intervention. At two days after hatching nestlings had to be weighed and measured. When the stone between the pit and the nest chamber was removed, the brooding adult bird directed spearing attacks with its bill at my hand or anything else that moved. Consequently, nestlings were sometimes stabbed and died from internal hemorrhaging. Subsequent mortality of this nature was eliminated by quickly removing the adult bird when the nest chamber was opened and returning the bird by way of the nest tunnel entrance after resealing the chamber.

Discounting deaths caused by human intervention, 97.2% of the nestlings (n= 69) were successful through the nestling period and fledged. Mortality due to natural causes was only observed in two nestlings. One nestling lost weight consistently and was emaciated at death. Whether death was due to starvation or parasitic infection was not determined. A second nestling died five days after hatching when an adult fed it a fish that was nearly the same size as the nestling (Figure 5). Presumably, the bird died of asphyxiation.

The death of one, two, or even three nestlings within a brood did not appear to alter the rate of growth or development of the surviving young. Broods having only three or four young fledged at the same age as broods comprised of six or seven young.

Figure 5

A nestling that presumably choked to death after being fed a large minnow. The tail of the fish extends from the bill of the nestling. Note the swollen esophagus.



GROWTH AND DEVELOPMENT OF NESTLINGS

Kingfishers are among the few sub-passerine species whose young are hatched in the blind, nidicolous, and psilopaedic condition. At hatching, the nestlings are without any trace of natal down and weigh from 9-13 grams (Figure 6a). For the first four days after hatching, the young are constantly brooded by one parent.

Although nestling kingfishers may remain in the nest for 27-29 days after hatching, the rate of growth is relatively rapid. The instantaneous rate of growth for nestling kingfishers was greatest during the first 10 days after hatching (Figure 7). Morton and Carey (1971) found that the highest rate of growth in the White-crowned Sparrow occurred during the first five days after hatching.

Nestling kingfishers achieved the range of adult body weights by 16 days after hatching (Figure 8). Unlike the altricial young of many passerine species, nestling kingfishers continue to gain weight until 18-20 days after hatching, and may surpass adult body weight during the nestling period. During the last week of the nestling period, nestlings lose weight and weigh less than adult birds when they leave the nest.

Among passerines, the rate of growth usually decreases with age (Dawson and Evans, 1957, 1960; Maher, 1964; Yarbrough, 1970; and Morton and Carey, 1971). In some swallows, however, the patterns of growth are similar to those of the Belted Kingfisher (Stoner, 1935, 1945; Lunk, 1962). As in passerine species, standard measurements of culmen length and wing length (from the wrist to the end of the third digit) of nestling kingfishers indicated a decrease in the rate of growth with increasing age (Figure 9; Figure 10).

By five days after hatching, all feather tracts showed the first signs of development and the eyes were beginning to open (Figure 6b). The young were no longer brooded by adults and for the first time were fed whole rather than partially digested fish.

Development of the humeral tract was more rapid than the development of other feather tracts. The humeral tract erupted by six days after hatching and by 13 days after hatching, the feathers were partially unsheathed and covered the dorsal surface of the body (Figure 11a). As the remaining feather tracts continued to develop and unsheath, the nestlings moved more freely about the nest and ventured into the nest tunnel.

The nest chamber was actively enlarged by the nestlings, and by fledging increased to 16 inches in diameter. Although the adults were never observed removing fecal sacs, the nest remained relatively unfouled throughout the nestling period. Nestlings backed against the nest wall prior to defecation. Following defecation, a nestling turned facing the wall and proceeded to peck at the soil above the fecal dropping. In this manner, the excreta was immediately covered and fouling of the nest was prevented. Kilham (1974) observed similar rapping behavior with captive nestling kingfishers but found that the rapping had no relation to places where excreta had landed.

By 16 days after hatching, almost all of the contour feathers were unsheathed and covered the apteria (Figure 11b). Remiges and rectrices remained sheathed, however, and the remaining 10 days in the nest were marked by complete development of the flight feathers. By fledging, flight feathers had developed sufficiently that a nestling was capable of sustained flight.

Figure 6

a. Newly hatched kingfishers.

b. Kingfisher nestlings at 5 days after hatching.

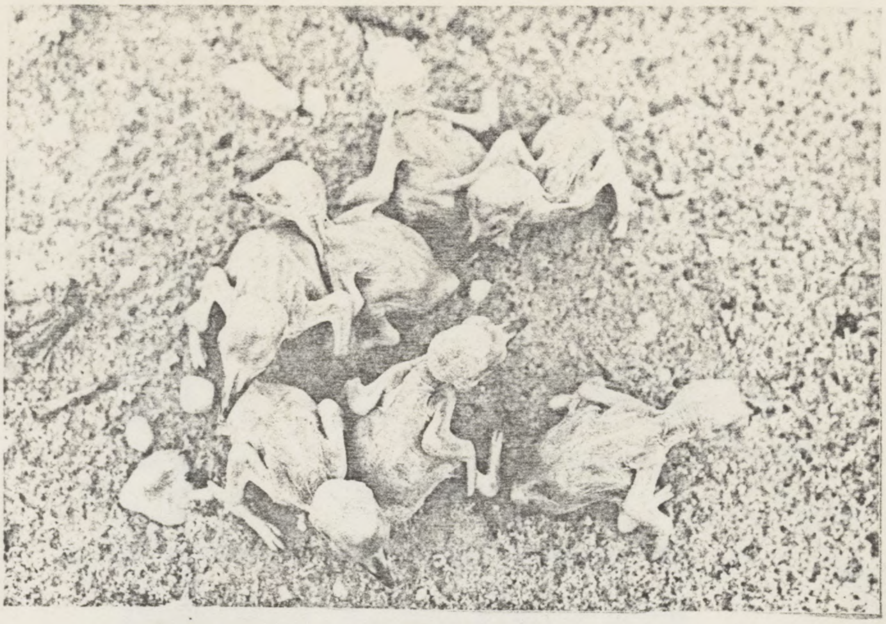


Figure 7

The instantaneous rate of growth for a brood of five nestling kingfishers. The points represent mean body weights. The numbers in parentheses are the growth rates (r) calculated by $\ln W_2 - \ln W_1$ where W is the mean body weight for a particular age.

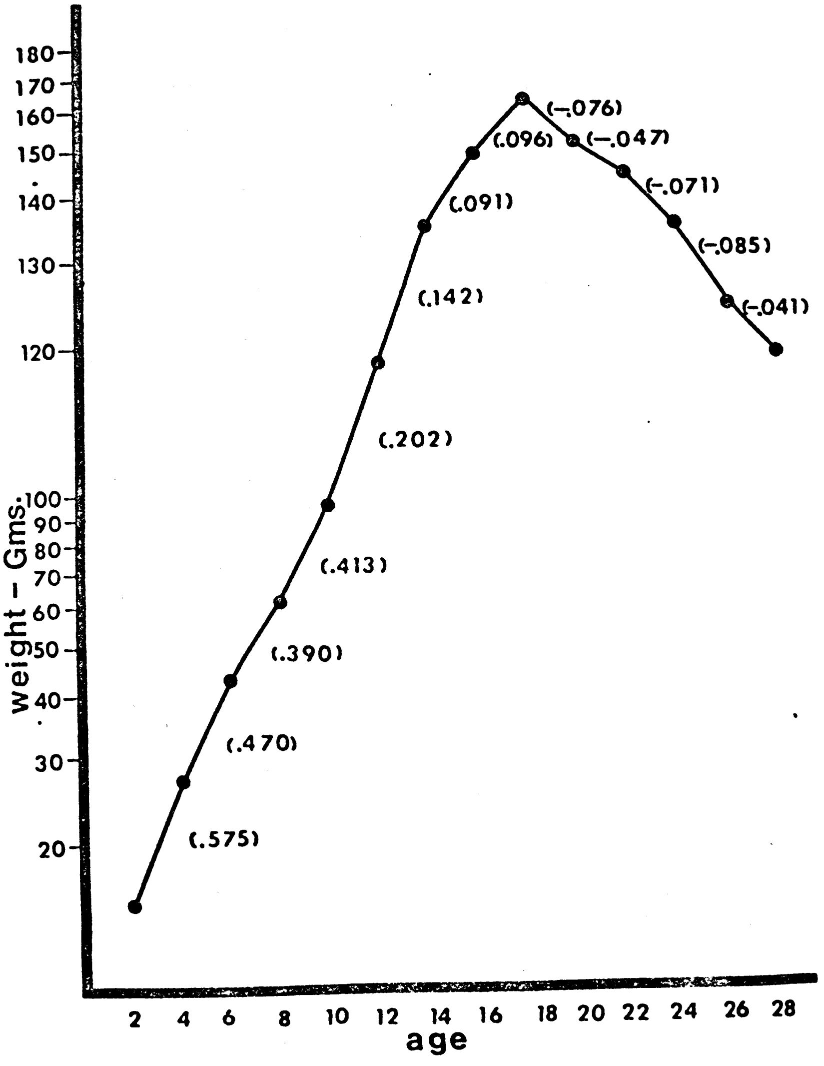

180
170
160
150
140
130
120
100
90
80
70
60
50
40
30
20
weight - Gms.
2
4
6
8
10
12
14
16
18
20
22
24
26
28
age
(.575)
(.470)
(.390)
(.413)
(.202)
(.142)
(.091)
(.096)
(-.076)
(-.047)
(-.071)
(-.085)
(-.041)

Figure 8

Growth of kingfishers throughout the nestling period. The points indicate the mean. The vertical lines represent the range of body weights, and the boxes represent 95% confidence interval estimates of the mean ($SE_x \times t_{.025}$).

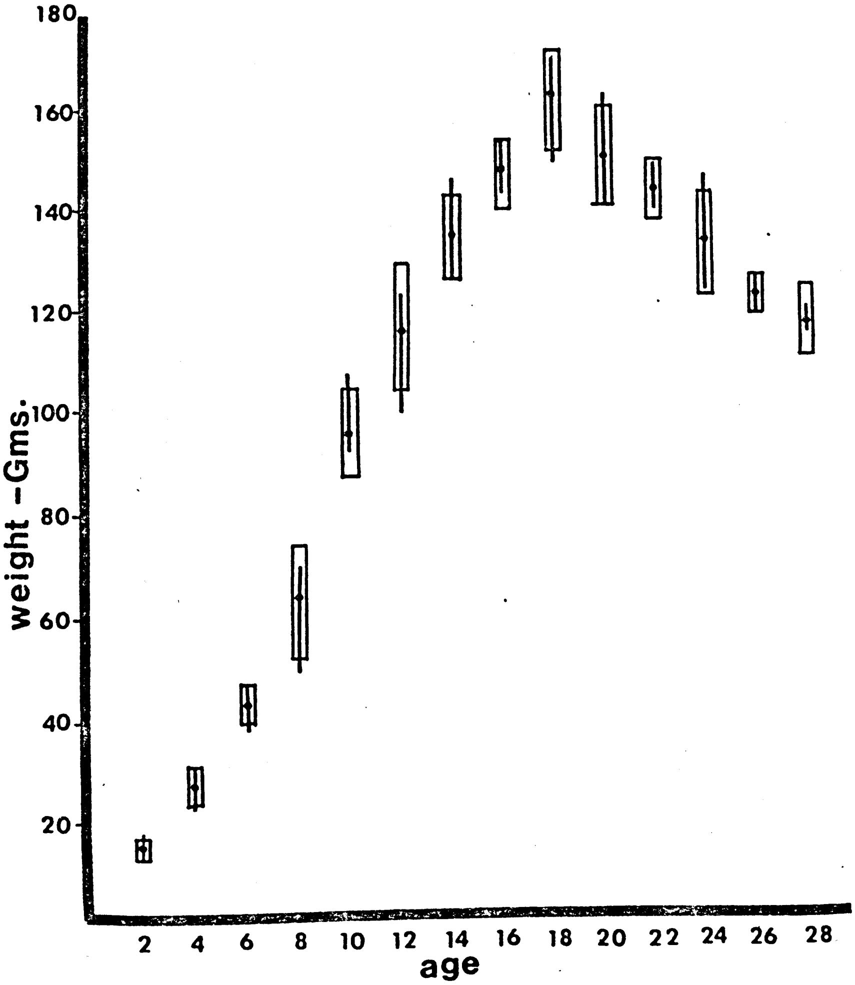

180
160
140
120
100
80
60
40
20
weight -Gms.
2
4
6
8
10
12
14
16
18
20
22
24
26
28
age

Figure 9

Culmen growth throughout the nestling period. The points indicate the mean. The vertical lines represent the range of culmen lengths, and the boxes represent 95% confidence interval estimates of the mean ($SE_{\bar{x}} \times t_{.025}$).

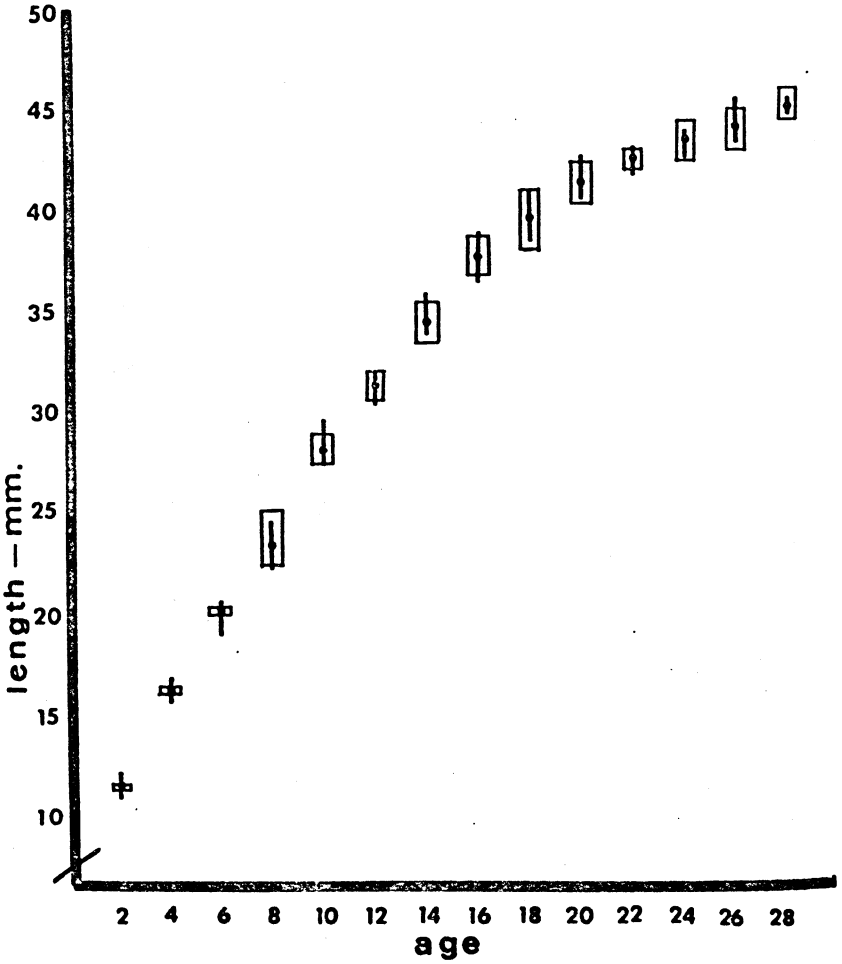

length — mm.
50
45
40
35
30
25
20
15
10
2
4
6
8
10
12
14
16
18
20
22
24
26
28
age

Figure 10

Wing growth of kingfishers throughout the nestling period. The points indicate the mean. The vertical lines represent the range of wing lengths, and the boxes represent 95% confidence interval estimates of the mean ($SE_{\bar{x}}$ X $t_{.025}$).

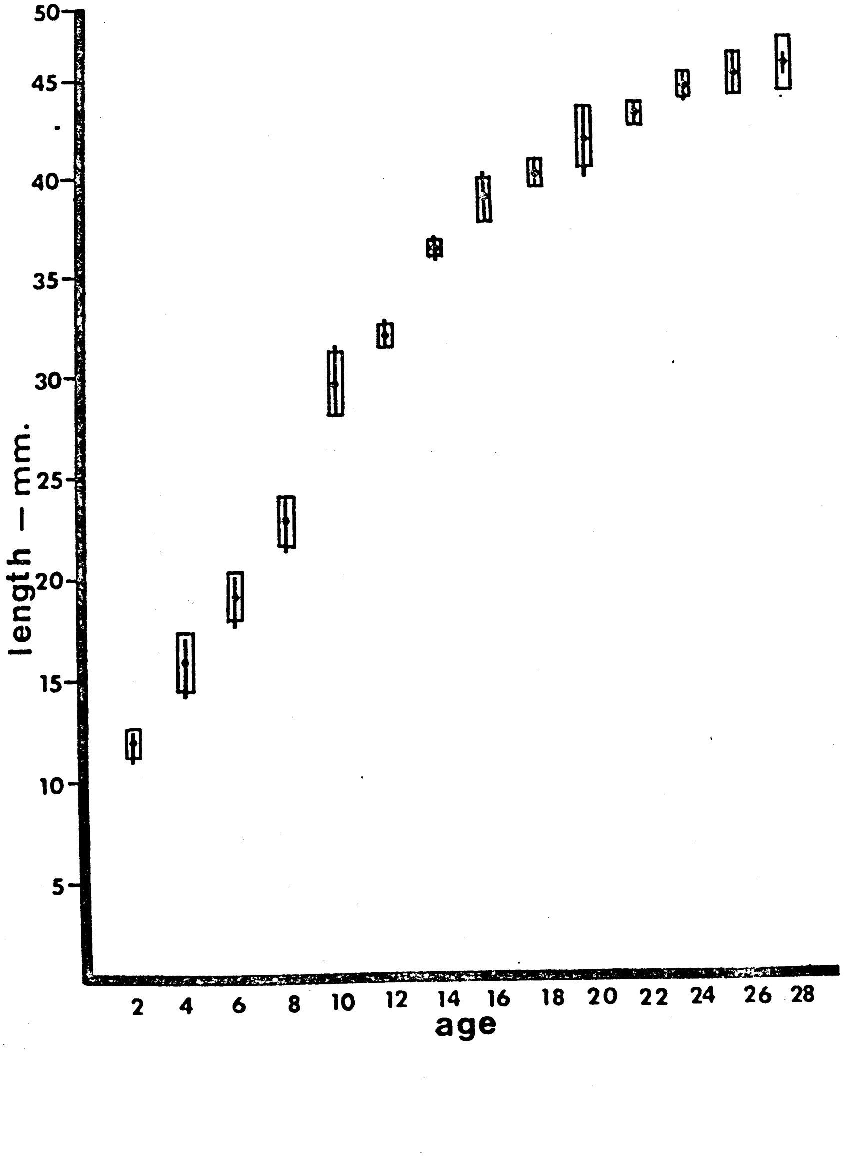
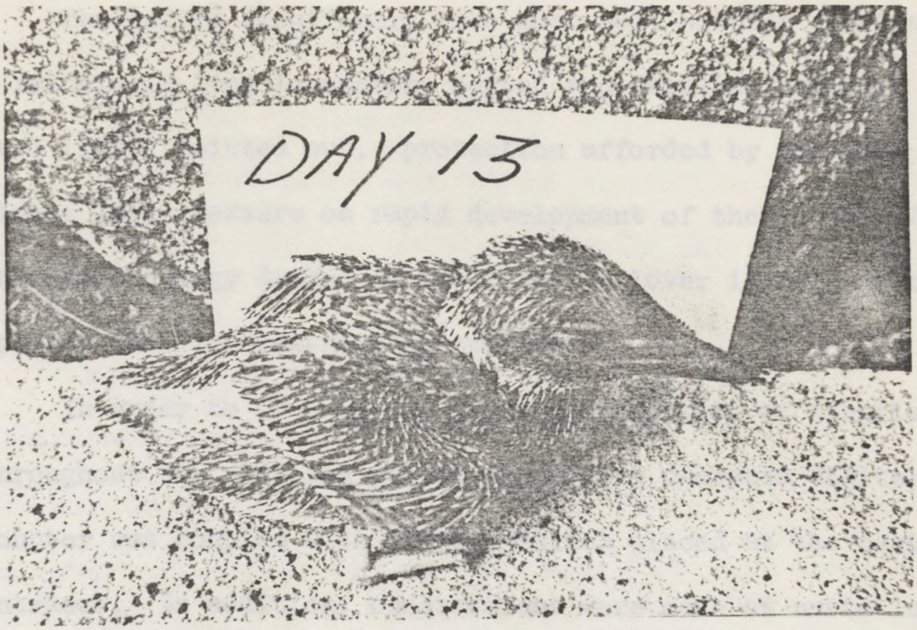

50
45
40
35
30
25
20
15
10
5
length — mm.
2
4
6
8
10
12
14
16
18
20
22
24
26
28
age

Figure 11

a. A kingfisher nestling at 13 days after hatching.

b. A kingfisher nestling at 16 days after hatching.


DAY 13

FEEDING ENERGETICS

The Belted Kingfisher, like most hole-nesting species, has a relatively long incubation period and nestling period. As Lack (1968) pointed out, protection afforded by the nest places less pressure on rapid development of the young. Therefore, the daily energy demand of nestlings is lower in hole-nesting species than in open-nesting species.

In order to observe the feeding energetics of kingfishers throughout the nestling period, a battery operated digital counter was coupled with a micro-switch placed at the nest entrance. In addition, observations were made at nests in order to determine at what time of day most feeding occurred and whether one parent assumed most of the feeding responsibilities.

From three to four days after hatching, only one adult procured food for the young while the other adult brooded. When an adult returned to the nest, no fish were held in the bill. In one instance, the male returned to the nest with no visible prey, but after entering the nest chamber, regurgitated six partially digested fish which both adults fed to the nestlings. Whole fish in the bills of adults were not observed until four to five days after hatching. Therefore, the absolute number of fish fed to nestlings during the first few days after hatching could not be determined.

At four days after hatching, adults returned to the nest with one fish per feeding trip. The number of fish per nestling per day could then be determined indirectly (Figure 12). Most feeding occurred during the morning and early evening hours.

Few feeding trips, if any, were made from 12:00 hours to 16:00 hours. Mousley (1938) likewise noted that the nest was occasionally unattended by the adults for as long as 2.5 hours.

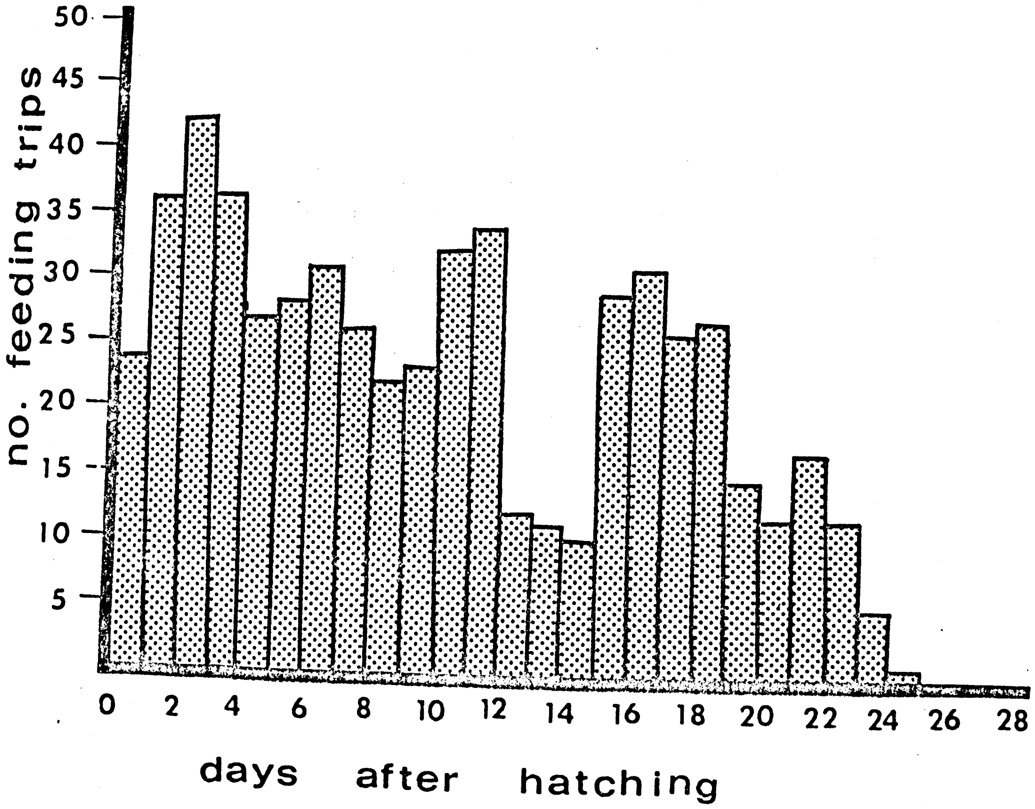
Most of the feeding was by the male. Observations at two nests showed that males made 63% of the feeding trips at each nest. Mousley (1938) found that the male made 67% of the feeding trips.

Results from a nest coupled with a digital counter indicated that the average number of fish fed per nestling per day from 5-18 days after hatching ranged from 3-5 with the exception of a three day period. From 13-15 days after hatching, the number of feeding trips was greatly reduced. During this time, violent storms may have hindered the adults from successfully catching fish due to torrential rains and strong winds.

From 19 days after hatching until fledging (28 days after hatching), feeding trips decreased markedly. In fact, the young were not fed after the twenty-fourth day. Concurrently, body weight of nestlings decreased (Figure 8). During the last few days in the nest, nestlings called from the nest entrance while an adult, often with a fish in its bill, called from a nearby tree. The call of the adult was the typical kingfisher rattle, but the young gave a short repetitive guttural rattle. These "begging calls" were the same as those given by captive nestlings reared during the summer of 1972. Whenever captive nestlings were approached by a human holding a fish, they gave the short guttural call. The same call was usually given when the birds were approached by a human not holding a fish.

Figure 12

The number of feeding trips per day at a Belted Kingfisher nest.


no. feeding trips
50
45
40
35
30
25
20
15
10
5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
days after hatching

FLEDGING AND POST-FLEDGING ACTIVITIES

From 27-29 days after hatching, nestlings leave the nest and are led by the adults to the fishing territory which may be as far as 1.5 miles from the nesting area. Upon emerging from the nest, the young are capable of flight and readily fly several hundred feet before lighting on an available perch. The adults remain in the nesting area until all nestlings have left the nest, and the family group remains in close contact as they move toward the fishing area. Both the parents and the young give contact calls of short rattles as the group moves through the forest.

Throughout the first week at the fishing territory, the young are fed by the adults but not regularly. Young birds usually sit on a low branch overhanging shallow water where they feed on crayfish. Salyer and Lagler (1946) found that after leaving the nest, the first food of young kingfishers was insects, particularly mayflies, and crayfish. Broods observed by Salyer obtained insects by "hawking" in the characteristic fly catcher manner. Wetmore (1964) reported that the adults often killed a fish and let it float on the water as a "practice" target for the young. Neither of these behavioral activities were observed during this study.

Young kingfishers do not need to be taught how to capture prey as reported by Brailer in Bent (1940). In 1972, four nestling kingfishers were reared in captivity in an outdoor flight cage. A large rectangular container filled with water was placed on the floor of the cage and throughout the day, both live and dead minnows as well as crayfish and dragonfly nymphs were placed in the container. The young birds readily took crayfish, dragonfly nymphs, and dead minnows, but it was several days before they captured a live minnow. Kilham (1974) likewise noted that young captive kingfishers did not take live minnows until one week after fledging. Although the cage was a highly artificial situation, such observations may reflect the early feeding habits of recently fledged kingfishers under natural conditions.

Circumstantial evidence suggests that predation on young kingfishers occurs during the first three weeks after fledging. On no occasion was an entire brood observed with the adults at the fishing area by the end of the first week after fledging. Predators at the nest in the Itasca Region are practically non-existant, but immediately after fledging young birds are not strong nor agile fliers and are likely prey items for birds of prey.

Bent (1940), White (1953) and Cornwell (1958) reported that accipiter hawks prey on kingfishers. Accipiter hawks and owls are common in the Itasca Region and Cornwell (1958) reported finding a dead juvenile kingfisher that had been preyed on by a Cooper's Hawk. No avian predators or remains of juveniles were observed during the course of this study and the causes of mortality among kingfishers are still a matter of conjecture.

By three weeks after hatching, family groups break up and juvenile birds leave the fishing territory of the adults. Although juvenile birds have the same plumage as adults, they could be identified since the bill was not yet as long as that of adult birds. Immature birds were frequently observed near roadside drainage ditches or culverts that had been previously unoccupied by kingfishers during the breeding season. In all instances, immature kingfishers were observed singly.

PHYSIOLOGICAL ADAPTATIONS FOR BREEDING

INTRODUCTION

All organisms must respond to temperature, regardless of where they live. Moreover, temperature is a fundamental physical factor affecting the geographic distribution of animals and plants alike, and ultimately, thermal adaptation is a manifestation of selection for physiological fitness, since even the optimal efficiency of enzyme regulatory systems is profoundly affected by temperature. If an organism cannot respond to the thermal variations in a given environment either behaviorally, morphologically, and/or physiologically, it will perish.

The original terminology describing the thermoregulatory capabilities of animals was dichotomous. Either an animal was cold-blooded; a poikilotherm, or warm-blooded; a homeotherm. Among vertebrates, the fishes, amphibians, and reptiles were designated as poikilotherms, and the birds and mammals were homeotherms.

Interpretation of homeothermy and poikilothermy can be subjective and sometimes misleading. Basically, the problem lies in semantics. Therefore, additional terminology such as regulator and conformer, and endothermy and ectothermy have been adopted when referring to the thermoregulatory capacities of animals.

Recent investigations have shown that several groups of animals, originally designated as poikilotherms, are in fact capable of effective temperature regulation (Heath, 1965; Keven and Shorthouse, 1970; Lillywhite, 1970; Carey, et. al., 1971; and Heinrich, 1972). On the other hand, some animals that have been traditionally regarded as homeotherms undergo periods of hypothermia or torpor, rather than maintaining constant body temperatures (Bartholonew, et. al., 1957; Tucker, 1962; Calder and Booser, 1973; Hudson, 1973).

The significance of thermoregulatory capabilities in animals should be viewed from the standpoint of mechanisms rather than from a phylogenetic relationship. It is without question that the mechanisms by which animals respond to their thermal environment vary considerably, but through the evolution of homeostatic regulatory systems, animals have become increasingly independent of their respective environments and thereby afforded the opportunity to colonize new habitats and develop new niches.

Birds have been highly successful in their adaptive radiation. They have colonized all the continents, oceanic islands, and the arctic ice cap where adaptations for survival have been manifested through behavioral, morphological, and physiological mechanisms. Adaptations for breeding have been essential for both adults as well as young birds, and the mechanisms by which young birds respond to their thermal surroundings are of particular significance in regard to the success of a species.

The phenomenon of temperature regulation is by no means a recent discovery to the scientific world. In the twentieth century, we sometimes fail to realize that the basis of much of our scientific investigation has its roots in all but forgotten observations of the past.

In 1839, Edwards noted that young birds could be relegated to one of two classifications in terms of their development at hatching. Such developmental conditions have come to be known as altricial and precocial, and young birds that are indicative of such stages of development have been regarded as nestlings and chicks respectively. In addition to describing feather development at hatching, Edwards further noted that a basic physiological difference existed between the two types of newly hatched birds. Altricial young comprised that group that are hatched with naked skin and which cool in the same manner as cold-blooded animals. Precocial young included those birds that are hatched with a down covering and that maintain their body temperature at considerable elevation above ambient temperatures normally encountered during the breeding season.

Hailman (1973) has discussed the inconsistent interpretation of the terms altricial and precocial in the ornithological literature. In the context of this discussion, altricial will refer to those nestlings hatched with sparse down or without feathers, totally dependent on the parents for food, and incapable of leaving the nest for an extended period of time. Precocial chicks include those young hatched with a downy integument, but may or may not be capable of feeding by themselves or leaving the nest relatively soon after hatching.

During the nineteenth century, most accounts of temperature regulation mentioned birds incidentally. In 1898, Pembrey summarized most of the work that had been accomplished until that time, and the contributions of several investigators during the first half of the twentieth centure laid the basic foundation for subsequent research in avian thermoregulation (Simpson and Galbraith, 1905; Wetmore, 1921; Kendeigh and Baldwin, 1928; Ginglinger and Kayser, 1929; Baldwin and Kendeigh, 1932; Kendeigh, 1939; Odum, 1942).

Since 1950, the literature has become voluminous, and with the recent expansion of scientific disciplines, many students of temperature regulation have restricted their investigations to cellular, chemical, physical, and theoretical aspects. Such endeavors have contributed significantly to our knowledge of thermoregulation. However, at times basic observations of whole organisms interacting in their natural environment have been neglected.

The development of temperature regulation in young birds has been investigated in the field and/or in the laboratory (Bartholomew, et. al., 1953; Bartholomew and Dawson, 1954; Irving and Krog, 1956; Dawson and Evans, 1957; Farner and Severnty, 1959; Dawson and Evans, 1960; Howell and Bartholomew, 1961, 1962; Maher, 1964; Ricklefs and Hainsworth, 1968; Yarbrough, 1970; Morton and Carey, 1971; Dawson, Hudson and Hill, 1972; Hudson, Dawson, and Hill, 1974). Although the nesting habits and the surrounding thermal environments of the species studied thus far vary considerably, the above investigations have largely emphasized the mechanisms leading to the development of homeostatic thermoregulatory systems in temperature ranges usually encountered in the nesting environment.

It has been the purpose of this study to observe the development of temperature regulation in nestling Belted Kingfishers in the natural nesting environment as well as in the laboratory under controlled experimental conditions in order to evaluate the mechanisms by which homeostatic thermogenesis is achieved.

MATERIALS AND METHODS

Nestlings studied under controlled laboratory conditions were collected in the early afternoon and returned to the nest immediately after each experimental session. On no occasion was an entire brood removed from the nest, since the kingfisher is known to desert its nest (Cornwell, 1963). Ages of nestlings used in the laboratory ranged from 2-21 days after hatching.

In order to gain access to the nestlings, each burrow was excavated by digging a pit directly behind the nest chamber. After removing or replacing nestlings, a stone was placed in the opening between the pit and the chamber. The pit was then covered with fiber board and sod in order to discourage potential predators and to protect the nest from rain.

In the laboratory, nestlings were individually placed in polyvinyl containers in a thermostatically controlled chamber where they remained for at least 45 minutes before body temperatures were measured. Eleven nestlings were tested for their ability to thermoregulate at experimental ambient temperatures.

Body temperatures were measured at experimental ambient temperatures of 10^{o}, 20^{o}, 30^{o}, and $40^{o} \pm 1^{o}$ C. by inserting a thermistor probe (YSI No. 402) deep into the proventriculus within 10 seconds after the birds were removed from the chamber. All body temperatures were recorded by a telethermometer (Yellow Springs Instruments).

Temperatures were also measured at the nest. Permanently fixed mercury thermometers were inserted 15 centimeters into the soil directly above the nest chamber and at 15 centimeters above the ground surface. Nest chamber temperatures were measured with a telethermometer probe suspended from the top of the nest chamber so that no contact was made with young or adult birds.

In the field, body temperatures were monitored by temperature sensitive transmitters. The relatively recent development of various telemetry techniques has permitted the opportunity to measure physiological variables in organisms such that the organisms under observation are freely capable to respond to changing conditions in their respective environment. Furthermore, the use of transmitters permits a continuous monitoring of a physiological variable for extended periods of time without disturbance to the organism.

Transmitters, powered by mercury batteries, were obtained from the Mini-mitter Corporation, Indianapolis, Indiana. The transmitters were activated and functioned for two days before calibration since voltage output of mercury batteries can be initially greater at the onset of activation (Kuechle, 1967).

After embedding the transmitters in Elvax, a paraffin-epoxy mixture, (Dupont-De Nemours, Chicago), they were calibrated in a water bath. The wax-elvax coating insured that the electrical circuit of the transmitters would not be short circuited by water or animal body fluids

Transmitters were surgically implanted beneath the left lobe of the liver and just below the apex of the heart in nestlings of known ages. Pulses from the transmitters were received on the AM band of a pocket-sized radio electronically coupled with a timing mechanism and recorded on a battery-operated cassette tape recorder. Therefore, it was possible to monitor body temperature throughout the daytime and evening hours without physical disturbance to the young or to the nest.

Since battery life is limited as a function of temperature and time, transmitters were surgically removed from four to six days after implantation and taken to the laboratory for recalibration. The rate of drift was practically negligible for all transmitters during recalibration, and in most instances differed by a few thousandths or ten-thousandths of a second from the initial calibration values. Initial calibration pulse rates for 0.5° C. increments differed by tenths of seconds or more.

RESULTS

LABORATORY STUDIES OF THERMOREGULATION

Although nestling kingfishers remain in the nest from 27-29 days after hatching, their patterns of thermogenic development are similar to those of several passerine species that have been observed in the laboratory (Dawson and Evans, 1957, 1960; Maher, 1964; Ricklefs and Hainsworth, 1968). At hatching, nestlings are blind, helpless, and naked. Until nine days after hatching, nestlings lacked the capacity to maintain a constant body temperature when tested for their ability to thermoregulate under controlled ambient temperatures (Figure 13). Body temperatures increased with increasing ambient temperature from 10° C. to 40° C. in a typical "poikilothermic" manner.

Slopes of T_A X T_B were calculated by least squares regression where T_A was ambient temperature and T_B was body temperature of the nestlings. The body temperatures of nestlings five to seven days old very nearly approximated the experimental ambient temperatures, but they were not in equilibrium.

Comparison of the regression coefficient of T_A X T_B regression of the five to seven day old nestlings with a hypothetical regression coefficient of 1.0 showed a significant difference ($P < .025$). A regression coefficient of 1.0 could have been translated as equilibrium between body temperatures of nestlings and ambient temperatures.

Statistical analysis of the regression coefficients of nestlings five to seven days old and eight to nine days old showed no significant difference (Figure 14). At five days after hatching, nestlings were still without an insulative shell, although the feather tracts were showing signs of development. However, by nine days after hatching, pin feathers of the humeral tract had erupted. Nestlings showed no visible signs of shivering until six days after hatching.

A significant trend toward the capacity to thermoregulate, as compared with nestlings younger than nine days, occurred from 10-15 days after hatching. However, regression coefficients of two age groups of nestlings in the ten to fifteen day old age class showed no significant difference from each other.

By 15 days after hatching, papillae of all the major feather tracts had erupted or started to unsheath. The humeral tract was first to develop, hence forming the first assemblage of an insulative shell covering the back of the bird.

At ambient temperatures below 20° C., shivering was evident, and occasionally the birds flapped their wings. At 40° C., the wings were often extended perpendicular to the body and panting was observed in a few nestlings.

By 16 days after hatching, development of the contour feathers was practically complete and nestlings were capable of maintaining a relatively constant body temperature independent of the experimental ambient temperatures. At an ambient temperature of 10° C., the birds fluffed their feathers and sat on their tarsi. At 40° C., the birds did not pant or show signs of hyperthermia.

The regression coefficient for nestlings 16 to 21 days old was significantly different from all other age groups. Likewise, it was just significantly different from a hypothetical regression coefficient of zero. Zero would have indicated complete regulation at all ambient temperatures.

In the nest, body temperatures of 19 day old nestlings ranged from 38.2° C. to 39.4° C. at a nest temperature of 25.8° C. The mean body temperature was 38.7° C. (n = 3). Twenty-seven day old nestlings had consistent body temperatures of 41.0° C. (n = 3) when the nest temperature was 20.0° C.

Body temperatures of adult birds captured in the field were similar to nestlings 16 days or older. Body temperatures of 1 female and 2 males were 40.0° C., 42.2° C., and 42.7° C., respectively. Wetmore (1921) noted the body temperature of two adult male kingfishers as 39.2° C. and 40.0° C.

Figure 13

The relation of body temperature to ambient temperature in nestling kingfishers.

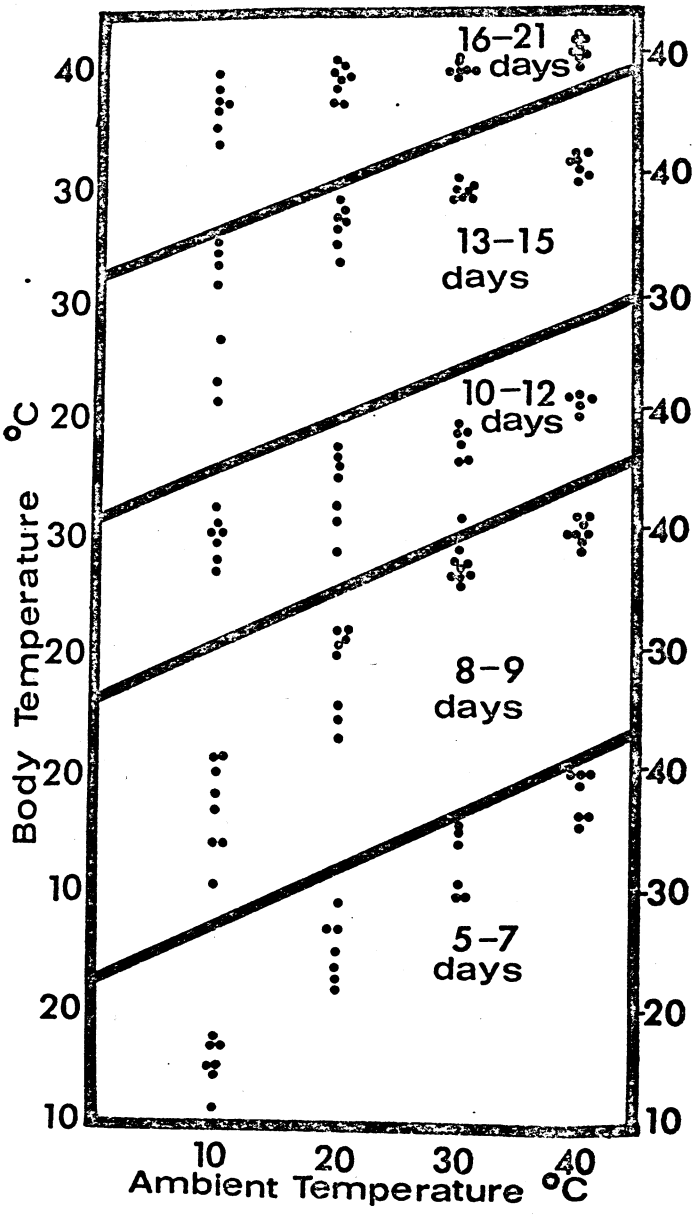
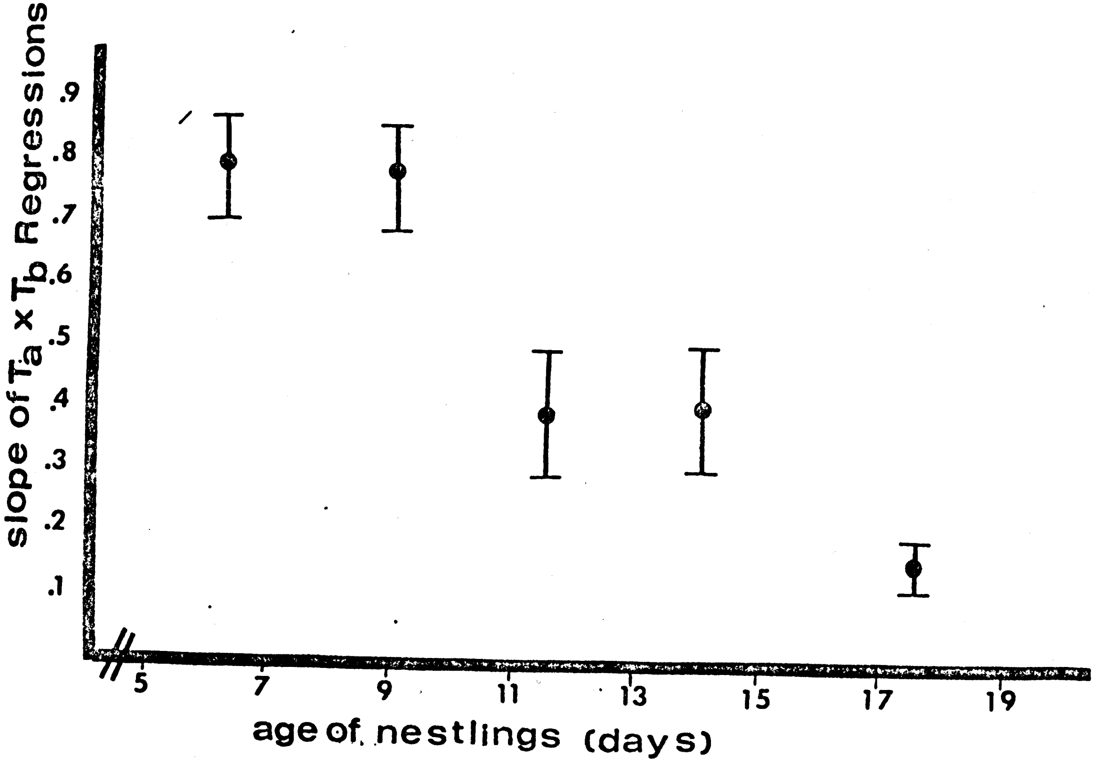

16-21 days
13-15 days
10-12 days
8-9 days
5-7 days
Body Temperature °C
Ambient Temperature °C
40
30
30
20
30
20
20
10
20
10
10
20
30
40
40
40
30
40
40
30
40
30
20
10

Figure 14

Slopes of T_A X T_B regressions with 95% confidence limits for nestlings at various ages.


slope of $T_a \times T_b$ Regressions
.9
.8
.7
.6
.5
.4
.3
.2
.1
5
7
9
11
13
15
17
19
age of nestlings (days)

RESULTS

TEMPERATURES IN THE NEST AND SURROUNDING ENVIRONMENT

The Belted Kingfisher nests in a subterranean burrow where ambient temperatures are not subject to wide fluctuation. Such a uniform micro-climate was observed throughout the nesting period.

Temperatures in the nest ranged from 14.0° C. to 20.5° C. at two days after hatching when one of the adults was brooding the young. However, ambient temperatures at 15 cm. above the ground surface ranged from 13.0° C. to 25.5° C. Fluctuations in ground temperatures were from 13.5° C. to 21.0° C. (Figure 15).

Similar thermal differences were observed at five days after hatching (Figure 16), 10 days after hatching (Figure 17), and 20 days after hatching (Figure 18). In all instances ambient temperatures outside the nest fluctuated several degrees from early morning until evening.

Variations in diurnal temperatures of the nest were never more than 06.5° C. and as the nestling stage progressed, these variations in nest temperature decreased. Diurnal temperatures in the soil, directly above the nest, showed similar fluctuations throughout the nestling period. In all instances, the soil was warmer than ambient air during the early morning hours. Likewise, when ambient temperatures dropped, particularly after sunset, there was a lag in the decline of soil temperature. The lag in temperature change was evident throughout the nestling period but appeared to be more dramatic in late June as compared to early June.

Daytime temperatures for a nest that had previously been occupied were more stable than temperatures of occupied burrows (Figure 19). Temperatures in the control burrow varied by only 0.5° C. Soil temperatures above the nest were lower than nest temperatures during the morning but increased later in the day and held constant while ambient temperatures decreased.

Figure 15

Temperatures in the nest environment two days after hatching.

T_a = ambient temperature 15 cm. above the ground surface.

T_n = nest chamber temperature.

T_g = ground temperature 15 cm. below the ground surface.

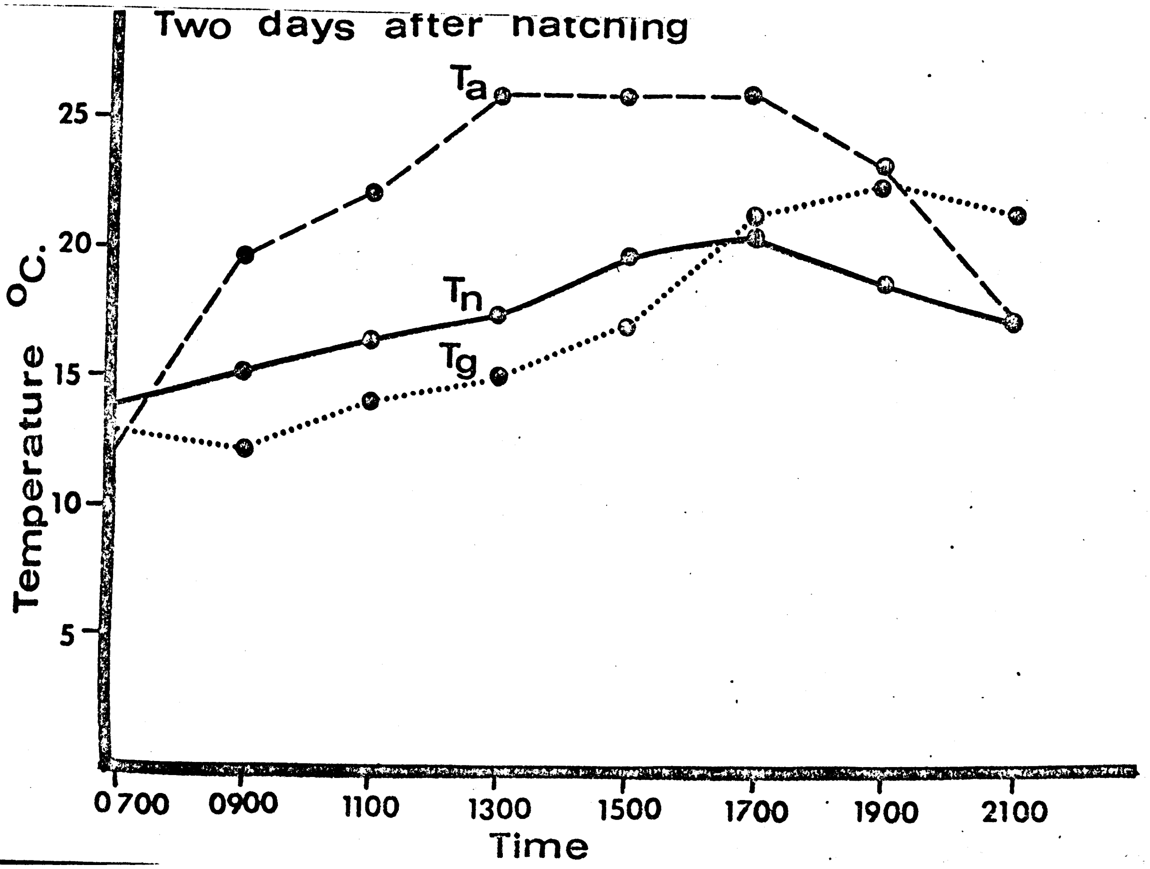

Two days after hatching
Ta
Tn
Tg
Temperature °C.
25
20
15
10
5
0700
0900
1100
1300
1500
1700
1900
2100
Time

Figure 16

Temperatures in the nest environment at five days after hatching.

T_a = ambient temperature 15 cm. above the ground surface.

T_n = nest chamber temperature.

T_g = ground temperature 15 cm. below the ground surface.

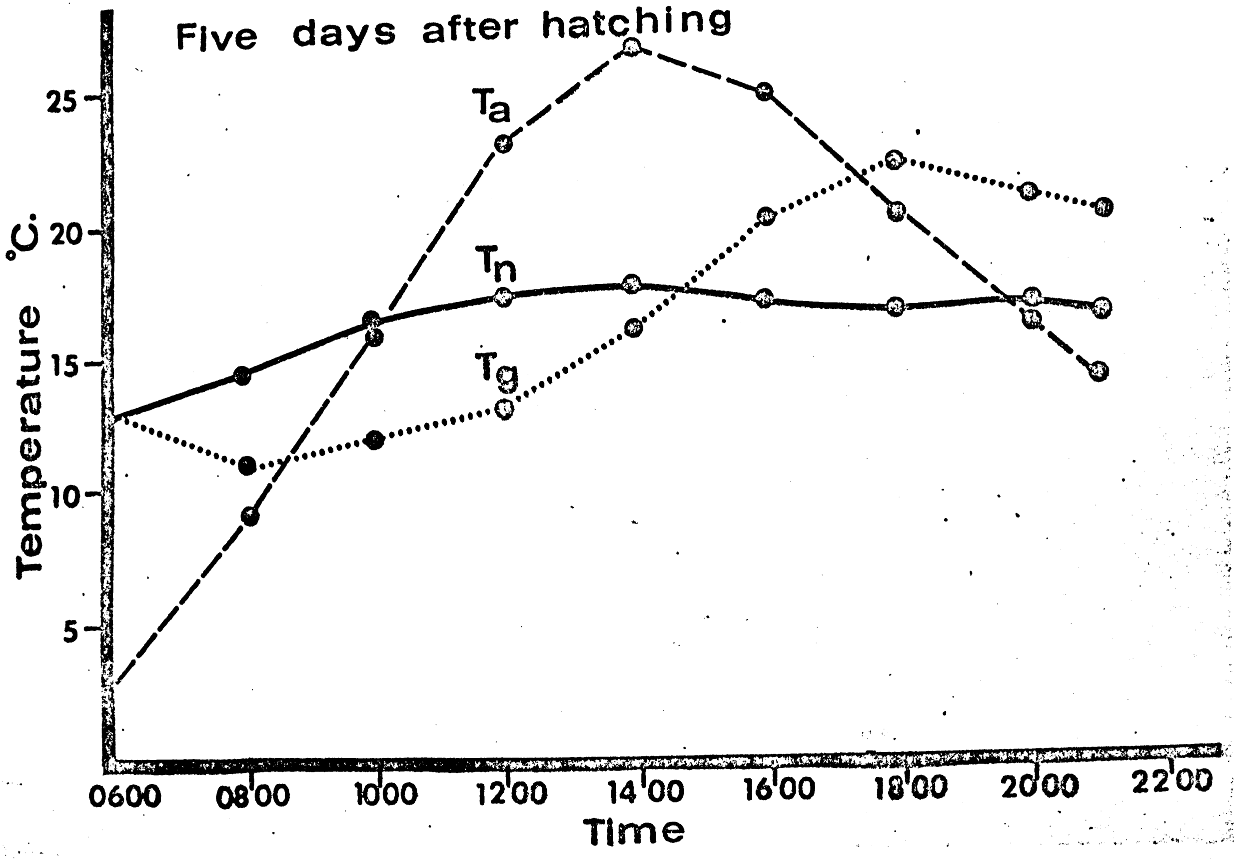

Five days after hatching
Ta
Tn
Tg
Temperature °C.
25
20
15
10
5
0600
08'00
1000
12'00
14'00
16'00
18'00
20'00
22'00
Time

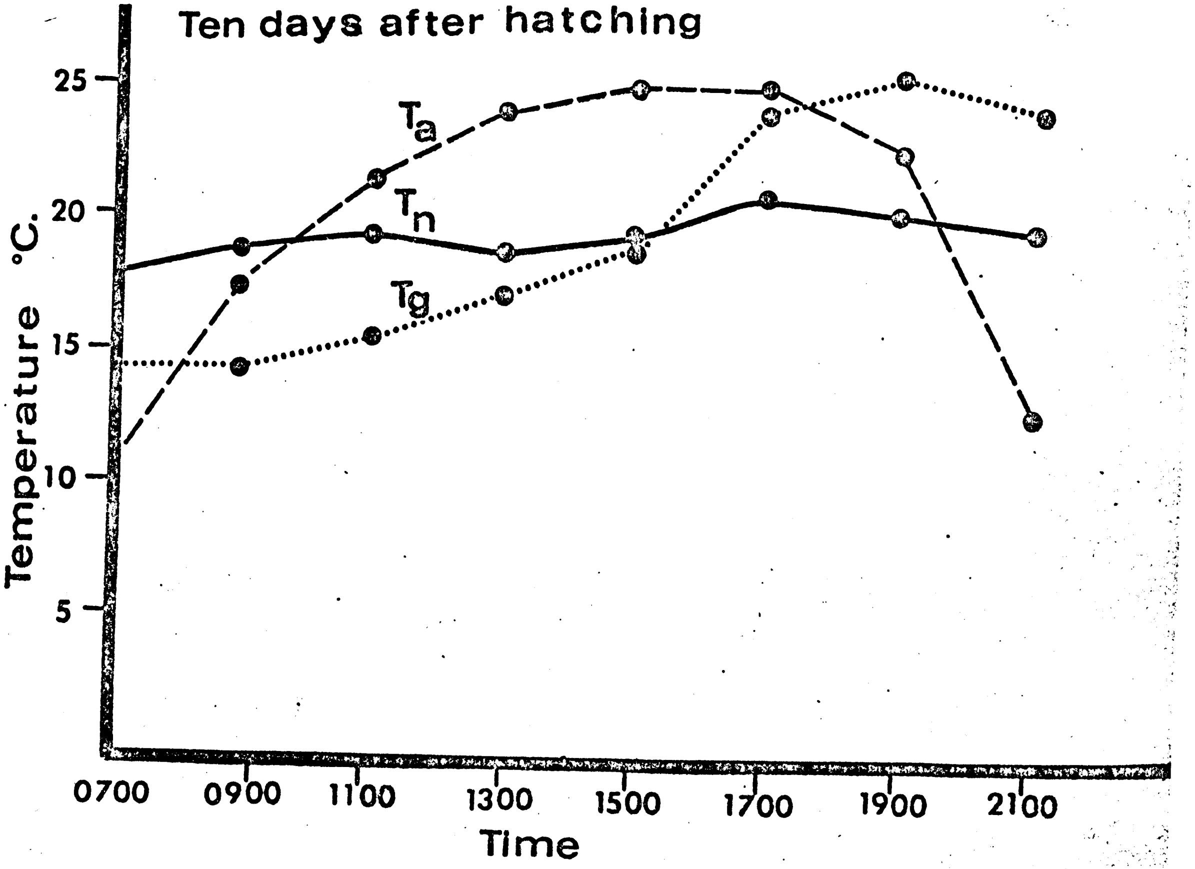
Figure 17

Temperatures in the nest environment at 10 days after hatching.

T_a = ambient temperature 15 cm. above the ground surface.

T_n = nest chamber temperature.

T_g = ground temperature 15 cm. below the ground surface.



Ten days after hatching

Figure 18

Temperatures in the nest environment at 20 days after hatching.

T_a = ambient temperature 15 cm. above the ground surface.

T_n = nest chamber temperature.

T_g = ground temperature 15 cm. below the ground surface.

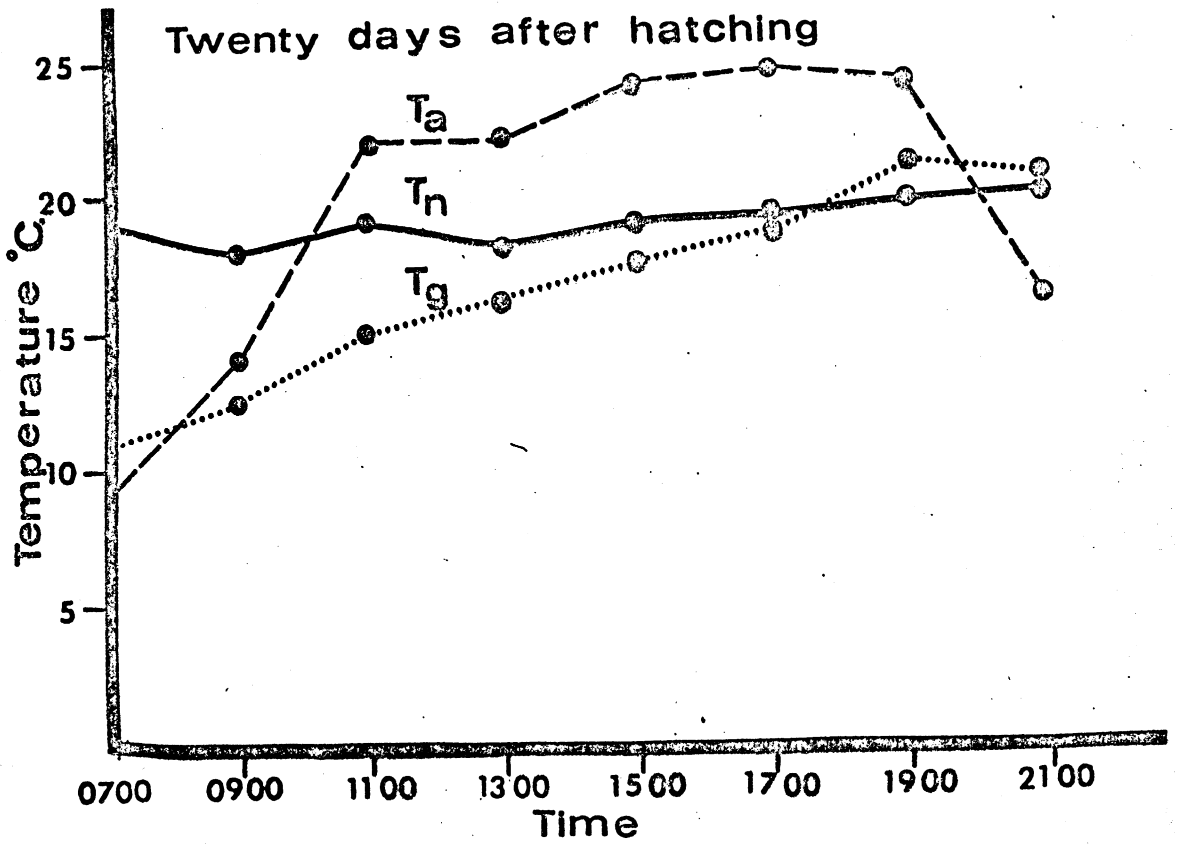
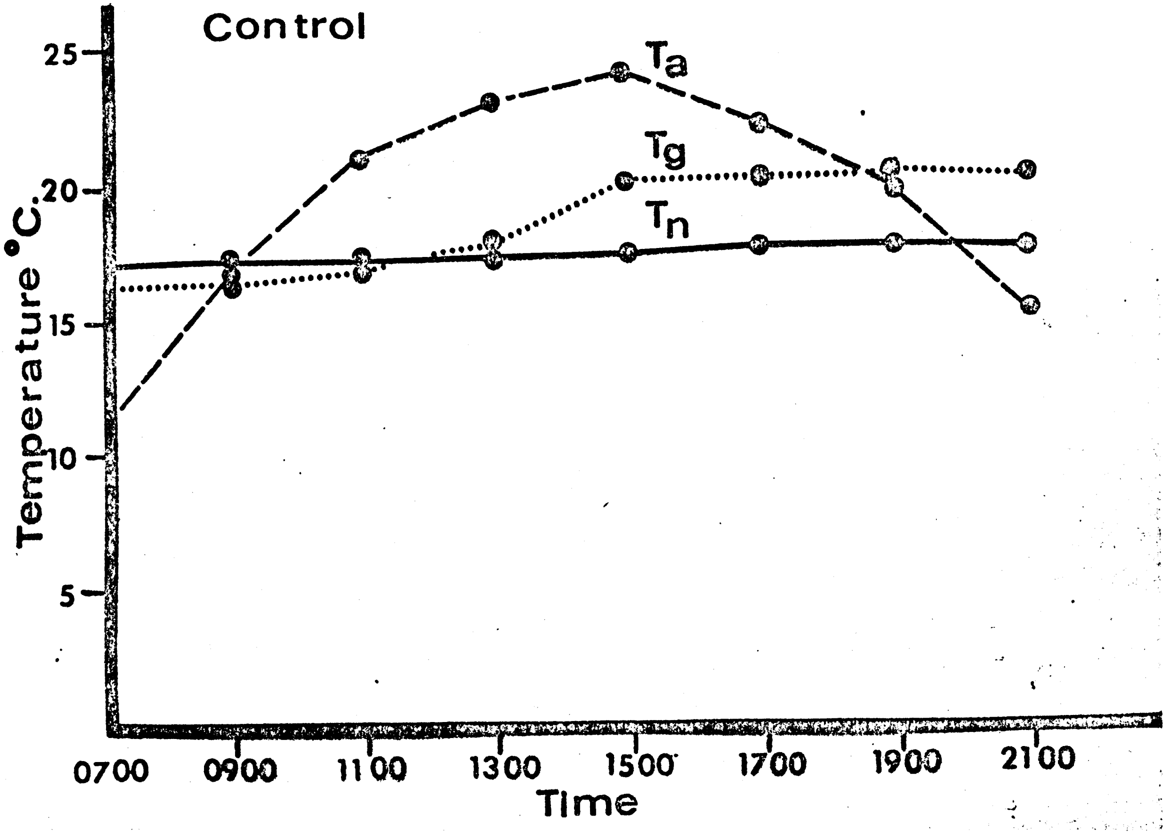

Twenty days after hatching
Temperature °C
25
20
15
10
5
Ta
Tn
Tg
0700
0900
1100
1300
1500
1700
1900
2100
Time

Figure 19

Temperature in a control nest environment. The nest had previously been active.


Control
Ta
Tg
Tn
Temperature °C.
25
20
15
10
5
0700
0900
1100
1300
1500
1700
1900
2100
Time

FIELD STUDIES OF THERMOREGULATION

Having observed the ontogeny of temperature regulation under controlled laboratory conditions stimulated enquiry regarding the development of thermogenesis under natural conditions of the nesting burrow. Data collected from the field were quite different from data obtained in the laboratory.

Body temperatures of a six day old nestling in which a transmitter had been surgically implanted showed a variation of 3.0° C. during a 36 hour period. Body temperature ranged from 37° C. to 40° C. (Figure 20). However, nestlings of the same age that had been tested for the capacity to thermoregulate in the laboratory had not been capable of maintaining a constant body temperature below an ambient temperature of 30° C.

At six days after hatching, nestlings were no longer brooded by either adult and papillae of the feather tracts were just beginning to erupt. Throughout the early stages of nestling development, however, the young were always huddled together whether during the daytime or late evening hours. When removed from the nest and placed in a circular arrangement, the nestlings vocalized and moved together forming a mass of closely interlocked heads and wings (Figure 21).

Body heat of nestlings helped to maintain nest temperatures well above ambient nighttime temperatures outside the nest (Figure 22a). After fledging, temperatures in the same nest were nearly the same as temperatures outside the nest (Figure 22b).

Body temperatures of a 14 day old nestling ranged from 39° C. to 40° C. for a 21 hour period with the exception of one reading (Figure 23a). By fourteen days after hatching, feathers of the humeral tract were unsheathed and feathers of the other major tracts were beginning to unsheath.

In a 21 day old bird, body temperatures remained relatively constant, and again, with the exception of one hourly reading, body temperatures did not fluctuate more than one degree during a 15 hour period (Figure 23b). By 21 days after hatching, all contour feather development was practically complete, and body temperatures were similar to those of adult birds measured in the field.

Initial analysis of transmitter data was confusing when body temperatures suddenly decreased in the 14 and 21 day old nestlings. However, it became apparent that the signal from the transmitter was relatively weak when the two low temperatures were recorded. Since the distance from transmitter to receiver affects the amplitude of the signal, it seemed likely to deduce that young birds were somewhere in the tunnel and not in the nest chamber with their siblings when the lower body temperatures were recorded.

Figure 20

Hourly body temperatures of a nestling from 6 - 8 days after hatching.

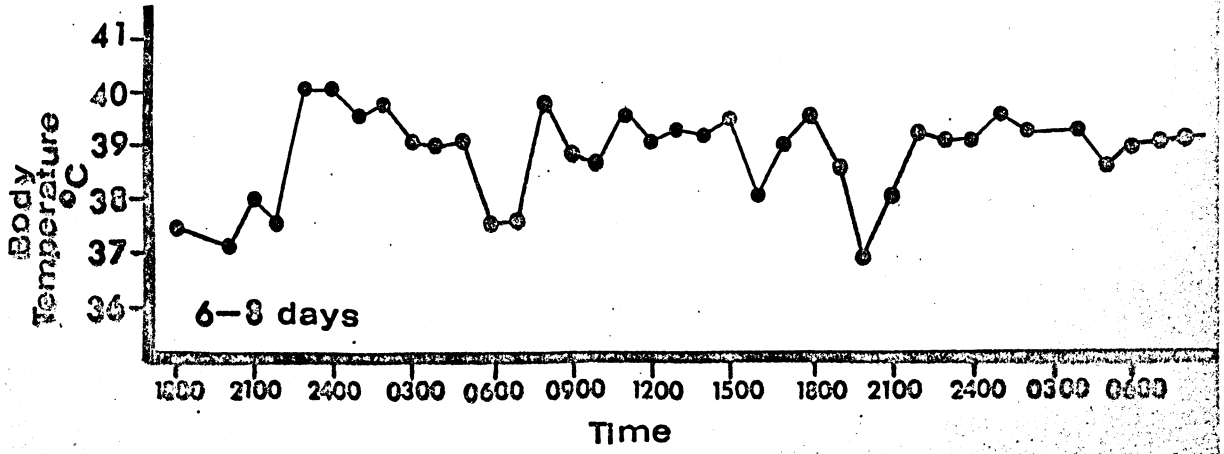

Body Temperature °C
41
40
39
38
37
36
6—8 days
1800
2100
2400
0300
0600
0900
1200
1500
1800
2100
2400
0300
0600
Time

Figure 21

Huddling behavior among a brood of kingfishers.

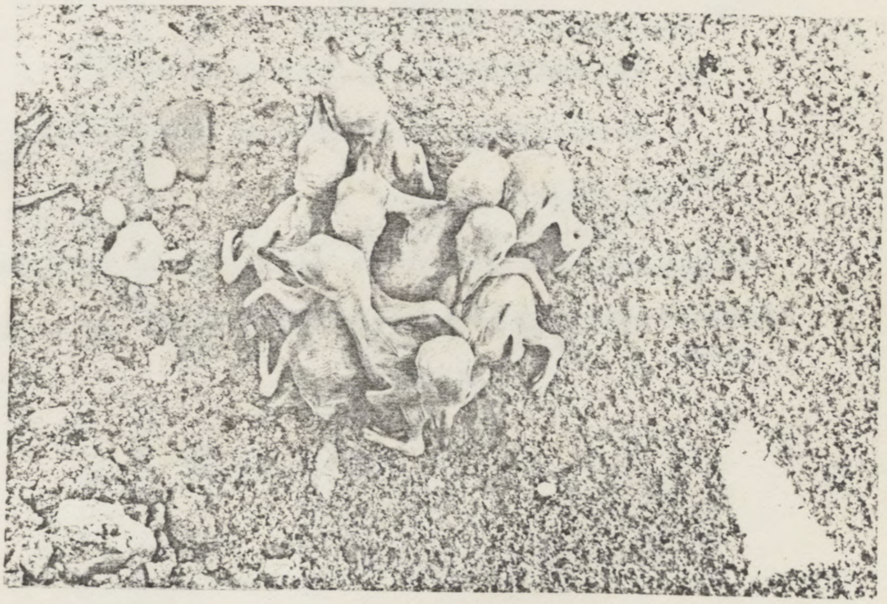
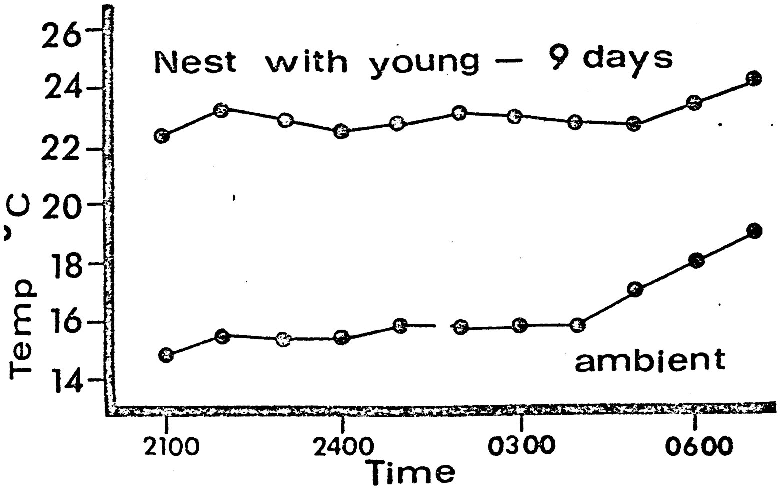


Figure 22

a. The maintenance of nest temperatures by nestlings above ambient temperatures outside the nest.

b. Temperatures of an empty nest in relation to ambient temperatures outside the nest.


Nest with young — 9 days
ambient
Temp °C
26
24
22
20
18
16
14
2100
2400
0300
0600
Time

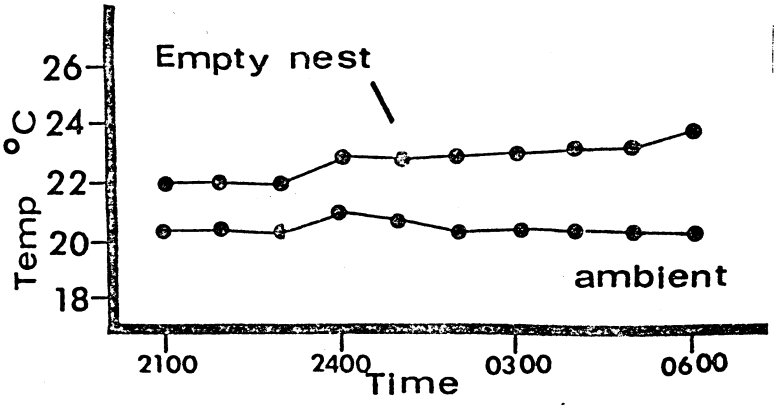
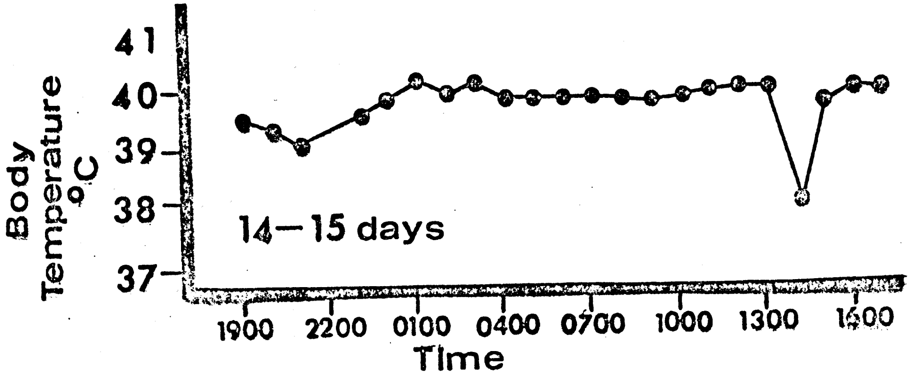
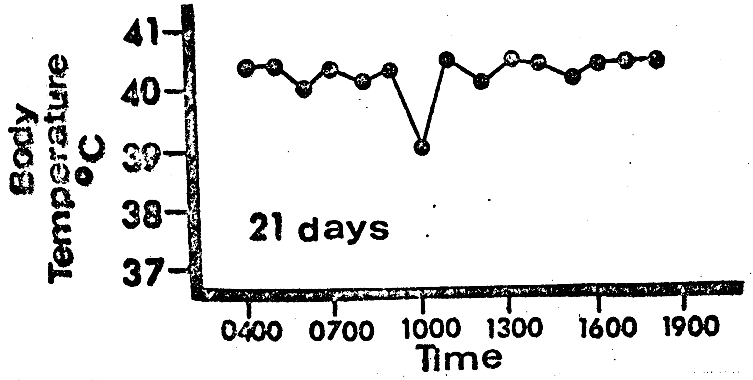

Empty nest
ambient
Temp °C
26
24
22
20
18
2100
2400
0300
0600
Time

Figure 23

a. Hourly body temperatures of a nestling from 14 - 15 days after hatching.

b. Hourly body temperatures of a nestling at 21 days after hatching.


Body Temperature °C
41
40
39
38
37
14—15 days
1900
2200
0100
0400
0700
1000
1300
1600
Time


Body Temperature °C
41
40
39
38
37
21 days
0400
0700
1000
1300
1600
1900
Time

DISCUSSION AND CONCLUSION

Traditionally, the development of temperature regulation has been observed in terms of what nestlings could do in the laboratory, rather than what was occuring in nature. In other words, observations of altricial nestlings under laboratory conditions have possibly yielded artificial and erroneous results. Consequently, ecological interpretations have been misconstrued.

Because the mechanisms and patterns of development leading to the establishment of thermogenesis are so complex, it is difficult if not impossible to observe and quantify all variables that are associated with an autonomous capacity to thermoregulate over a wide range of ambient temperatures. On the other hand, it can be dangerous to generalize, particularly regarding adaptations, when the scope of investigation has been limited to variables that have only been observed under controlled conditions.

Romanoff (1941) concluded from laboratory experiments that with altricial birds, mechanisms for control of body temperature did not become effective until several days after hatching. However, Irving and Krog (1956) maintained that although a nestling lacks sufficient energy and insulation necessary for independent homeothermy, it develops at temperatures nearly the same as in adults.

Investigations of factors influencing the development of temperature regulation have generally concluded that physiological endothermy cannot be fully attained until neuromuscular coordination and an insulative integument have developed.

Concurrently, a decrease in the surface area in proportion to body mass of growing nestlings reduces the stress of heat loss.

Among passerine nestlings, it has been shown that the establishment of effective thermogenesis appears to be related to growth and varies from species to species. Likewise, changes occurring in the surface-volume ratio of nestlings suggest an increase in skeletal muscle and therefore an improvement in motor ability (Dawson and Hudson, 1970). Furthermore, in some fringillids, the liver and heart grow at relatively more rapid rates than the rest of the body during the transition to physiological endothermy (Dawson and Evans, 1960). Therefore, delayed effectiveness of neuromuscular coordination and an insulative integument may be the result of allocation of additional tissue for internal growth during early nestling stages. Hence, the altricial condition has been regarded as highly adaptive in that development of the young occurs at a relatively rapid rate with a minimal expenditure of energy (Dawson, 1962).

Although the Belted Kingfisher is not a passerine, the patterns of growth and development leading to the establishment of homeostatic temperature control are relatively similar to those of passerine species. Under laboratory conditions, physiological endothermy of kingfisher nestlings occurred approximately half-way through the nestling period. These data are consistent with observations of Cactus Wrens where thermogenic homeostasis was evident at 10 to 12 days after hatching (Ricklefs and Hainsworth, 1968). Likewise, evidence of endothermy has been observed about half-way through the nestling period in the Vesper Sparrow, Chipping Sparrow, Field Sparrow (Dawson and Evans, 1957; 1960), and Snow Bunting (Maher, 1964).

In the Belted Kingfisher, the capacity for nestlings to maintain effective temperature control at experimental ambient temperatures below 30° C. did not occur until nine days after hatching. Although nestlings were without feathers, visible signs of shivering were evident by six days after hatching. Shivering responses, however, were still insufficiently coordinated to maintain a constant body temperature at low ambient temperatures. Odum (1942) observed no muscle tremors in the Black-capped Chickadee or House Wren at three days after hatching, but suggested that tremor heat production appeared to develop more rapidly than control of heat loss.

The significant transition to homeostatic thermogenesis in kingfishers occurred from 13-15 days after hatching and by 16 days after hatching, the manifestation of physiological endothermy was practically complete. At the same time, contour feathers had unsheathed thereby forming an effective insulative shell.

It has been well documented for altricial nestlings that homeostatic thermogenesis is largely the result of morphological and physiological aspects of development. There are no known reports of altricial nestlings fully capable of autonomous homeostatic thermogenesis at hatching, yet effective homeothermy is present immediately after hatching. Such apparent contradiction can be explained by the behavioral interactions among siblings in the nest or by interactions of adults with nestlings. Furthermore, insulative properties of the nest contribute as effective barriers to heat loss.

Results from surgically implanted transmitters and observations of nestling kingfishers in the nest show that effective homeothermy was manifested shortly after hatching. Body temperatures of a nestling, monitored via transmitter on an hourly basis from the sixth day after hatching through the eighth day after hatching, indicated that a relatively constant body temperature was maintained. However, nestlings of the same age that were tested for thermoregulatory capabilities in the laboratory lacked the capacity to maintain a constant body temperature below an ambient temperature of 30° C. Yarbrough (1970) examined the effects of environmental temperatures on nestling Gray-crowned Rosy Finches and concluded that the capacity of a brood to thermoregulate and the same capacity in individual nestlings were two distinct phenomena.

The major discrepancy in results obtained herein can probably be attributed to experimental methods. Kingfisher nestlings that had been tested in laboratory experiments were individually isolated in polyvinyl containers, whereas transmitter experiments were conducted under natural nest conditions. Consequently, isolation in polyvinyl containers provided neither insulation nor the opportunity for nestlings to interact with one another. Therefore, at ambient temperatures below 30° C., shivering could not sustain a constant body temperature. Under natural nest conditions, nestlings were not subjected to a wide range of temperatures, but developed in a relatively stable thermal environment as compared with ambient temperatures outside the nest burrow.

The question still remains, however, as to how naked nestlings were capable of maintaining body temperatures almost as high as those of adult birds. During the first four to five days after hatching nestlings were constantly brooded by one of the adult birds. A transmitter placed beneath a brooding adult on the second day after hatching indicated that young birds were in a thermal environment ranging from 35-57 degrees C. By the sixth day after hatching, adult brooding had terminated even during the evening hours, although the nestlings were still naked.

Nestlings facilitated their own thermogenesis through behavioral interactions with siblings in the nest. Baily (1900) reported that this huddling behavior lasted through nine days after hatching. By ten days after hatching, the humeral tract had begun to unsheath, and the greatest rate of growth had occurred by the tenth day. Undoubtedly, the changes in surface area-weight relationship played an additional role in conserving heat.

The nest, by definition, has been described as a receptacle for eggs (Pettingill, 1970), and whatever selective pressures were instrumental in prompting such a breeding strategy are open to speculation. In light of physiological adaptations, however, it is quite possible that the nest of many avian species provides an efficient barrier against heat loss such that nestlings can develop in a thermally stable environment.

Architecture of avian nests varies considerably, but in cupped receptacles, the loose packing of twigs, grasses, leaves, mud, etc. comprise a barrier of dead air spaces that are instrumental in retarding heat flow from the sides and bottom of the nest. Even when adult birds are not in attendance, temperatures inside the nest may be maintained above the ambient air temperatures, and with nestlings being tightly packed in the receptacle, an efficient canopy over the nest is formed. Edwards (1839) found that nestling sparrows had a body temperature four to five degrees lower than adults when contained in the nest, but if removed and isolated, they cooled with extreme rapidity. Yarbrough (1970) likewise found that a brood of young rosy finches could regulate its temperature in the nest at three days after hatching, but a single nestling could not although the nest cup was well insulated. Ricklefs and Hainsworth (1969) found that the nest of the Cactus Wren protected nestlings from both heat and cold, and the behavior of adults and young effectively moderated the nest environment.

The nesting strategy of the Belted Kingfisher is unlike that of most birds in that the nest consists of an excavated subterranean burrow having no lining other than a meager scattering of fish bones and scales that are regurgitated by the female during incubation. Therefore, for all practical purposes the nestlings are in direct contact with a bare earth substrate on all sides.

Thermal conditions in a hole-nesting environment provide a relatively stable micro-climate. Farner and Serventy (1959) reported a daily fluctuation in nest burrows of the Slender-billed Shearwater to be no more than five degrees C. For kingfishers, the nest chamber is sufficiently distant from the burrow entrance that it is not affected by fluctuations in ambient temperature outside the nest. Furthermore, high humidity in the nests tends to hold heat in a localized area, and spaces between soil particles form an efficient insulative barrier against heat loss. Some heat is likely to be lost by diffusing across thermal gradients, but with seven young in a somewhat spherical compartment, heat input is probably greater than heat loss. Another pathway of heat loss may have been due to convective flow that was induced by the adult movements into and out of the nest burrow.

Although avian nests may be efficient insulators, the body temperatures of nestlings may drop regardless of parental brooding during the evening. Gotie and Kroll (1973) found that in nestling Great-tailed Grackles, body temperatures declined throughout the evening but increased rapidly at sunrise when feeding re-commenced. The decline in body temperature throughout the night was attributed to decreases in digestive activity, muscular activity, and energy reserves.

Nestling kingfishers did not show a decline in body temperature but maintained a relatively constant body temperature throughout the night. Feeding did not occur after sunset, but perhaps fat reserves permit a normal metabolic activity to continue throughout the night. Prior to the development of an insulative shell, subcutaneous fat deposits were prominent on the ventral body surface of nestlings.

The brief decline in body temperature of a 15 and a 20 day old nestling occurred during the daytime but within an hour increased to previous values. The decrease in body temperature, in both instances, occurred when the birds were somewhere in the nest tunnel and not in the nest chamber with their siblings.

Generally, little data have been collected for hole-nesting species regarding the development of temperature regulation. This may be largely due to the inaccessability of nests. The data reported here indicate that in nature, nestling kingfishers are rarely if ever subjected to widely varying environmental temperatures. Certainly, the nest has contributed to effective temperature regulation of this hole-nesting species. Gardner (1930) reported that flickers appeared to form a curious exception among birds. He found that the body temperatures of newly hatched nestlings were as high as any subsequently measured. Even among open-nesting species, evidence has accumulated indicating that effective temperature regulation occurs immediately after hatching.

The thermoregulatory unit among newly hatched birds has been shown to be a highly integrated unit of great complexity. The nest, behavior among nestlings and adults, rates of growth and developmental aspects, shivering, etc. all contribute to a system that has been prompted by natural selection. An understanding of the mechanisms leading to homeostatic thermogenesis cannot occur in the laboratory alone, but in order to gain a full appreciation of the sequence of events, one must go to the field.

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APPENDIX I: SYSTEMATIC LIST OF COMMON AND SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT

Slender-billed Shearwater	*Puffinus tenuirostris*
Cooper's Hawk	*Accipiter cooperii*
Ringed Kingfisher	*Megaceryle torquata*
Belted Kingfisher	*Megaceryle alcyon*
Amazon Kingfisher	*Chloroceryle amazona*
Green Kingfisher	*Chloroceryle americana*
Half-collared Kingfisher	*Alcedo semitorquata*
Common Flicker	*Colaptes auratus*
Bank Swallow	*Riparia riparia*
Rough-winged Swallow	*Stelgidopteryx ruficollis*
Black-capped Chickadee	*Parus atricapillus*
House Wren	*Troglodytes aedon*
Cactus Wren	*Campylorhynchus brunneicapillus*
Great-tailed Grackle	*Cassidix mexicanus*
Gray-crowned Rosy Finch	*Leucosticte tephrocotis*
Vesper Sparrow	*Pooecetes gramineus*
Chipping Sparrow	*Spizella passerina*
Field Sparrow	*Spizella pusilla*
White-crowned Sparrow	*Zonotrichia leucophrys*
Lapland Longspur	*Calcarius lapponicus*
Snow Bunting	*Plectrophenax nivalis*